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The Great Basin Naturalist

VOLUME 46, 1986

Editor: Stephen L. Wood

THE GREAT BASIN NATURALIST
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1939

Published at Brigham Young University, by
Brigham Young University

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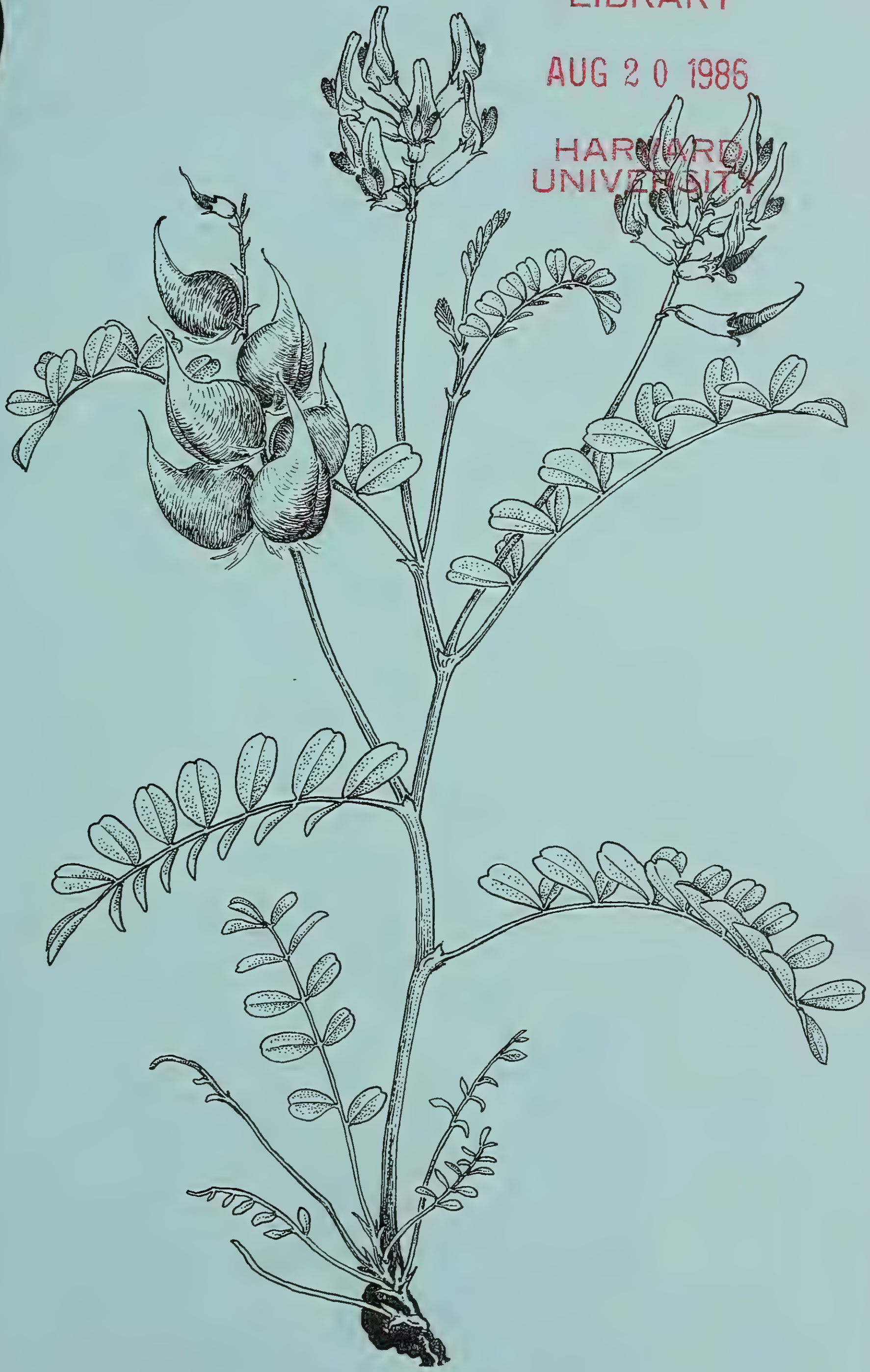

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Subscriptions. The annual subscription to the *Great Basin Naturalist* for private individuals is $16; for institutions, $24 (outside the United States, $18 and $26); and for student subscriptions, $10. The price of single issues is $6 each. All back issues are in print and are available for sale. All matters pertaining to subscriptions, back issues, or other business should be directed to Brigham Young University, *Great Basin Naturalist*, 290 Life Science Museum, Provo, Utah 84602. The *Great Basin Naturalist Memoirs* may be purchased from the same office at the rate indicated on the inside of the back cover of either journal.

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6-86 650 23497

ISSN 017-3614

The Great Basin Naturalist
PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 46 31 January 1986 No. 1

DYNAMIC LANDFORMS AND PLANT COMMUNITIES IN A PLUVIAL LAKE BASIN

James A. Young[1], Raymond A. Evans[1], Bruce A. Roundy[2], and John A. Brown[3]

ABSTRACT.—Mapping units were developed based on landform, soils, and plant communities for the 40,000 ha of salt desert vegetation located below the maximum level of pluvial Lake Gilbert in Grass Valley, Nevada. Lake plain, beach, and bar features of the pluvial lake provide the dominant landforms. Fine textured lake sediments have produced salt- and Na-affected soils. The distribution and structure of plant communities are related to depth of the groundwater table, fluctuations in this depth, and the salt content of the groundwater. Wind and water erosion combine to continually evolve new environments for colonization by plants in this ecosystem.

The structure and association of plant communities occupying basins in western North America that were formerly inundated by pluvial lakes has long been of interest to ecologists (Shantz and Piemeisel 1940, see West 1983 for description of ecosystems). The progressively finer textured soils from the edge of the basins and increasing concentration of soluble salts that formed as the lakes dried offered the potential of relating plant communities to soils, and especially to the salt content of soils (Kearney et al. 1914, Clements 1920, Billings 1945). Such salt-plant community orientations are complicated by the extreme aridity of many pluvial lake basins. In the Great Basin of the western United States, the entire province is located in the rain shadow of the Sierra Nevada and the Cascade Mountains. In addition, the mountains that rim many of the subbasins range from 2,150 to more than 3,000 m in elevation, casting their own rain shadows across the arid bottoms of the valleys (Houghton et al. 1975). The result is that the natural vegetation of the valley bottoms may reflect lack of atmospheric precipitation as much as the reduced osmotic potential of soil water solutions (Billings 1949).

The concept of pluvial basins containing concentric rings of soils with increasing salt content helps explain the distribution of many salt desert plant communities (Flowers 1934). The occurrence of other plant communities such as those dominated by *Ceratoides lanata* or *Atriplex confertifolia* is not associated with specific soil features (Gates et al. 1956). The distribution of *Atriplex nuttallii* on soils from low to high salinity is a good example of ecotypic differences within a species in relation to salt tolerance (Goodman 1973). Genetic differences must be considered when relating plant distribution to edaphic factors in the salt desert. Stutz (1978) has presented evidence that the new habitats provided by the drying of pluvial lake basins provide space for the explosive evolution of perennial species of *Atriplex*. Some of the landscape occupied by species of *Atriplex* exist in complex polyploid series. These desert landscapes dominated by woody chenopods apparently have limited regeneration and appear, superficially, to be composed of nearly identical individuals. According to Stutz's hypothesis, the endless sameness of woody chenopods is a mirage concealing dynamic evolutionary processes.

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[4] Plant names based on Cronquist et al. (1972) and Munz and Keck (1968). Plant specimens on file USDA/ARS Herbarium, Reno, Nevada.

Distinct patterns of vegetation on pluvial lake sediments were postulated by Miller et al. (1982) to be due to differences in soil-water-plant relations. Differences were caused either by the depth to groundwater or from differences in water-retention capacities of soils deriving water only from precipitation.

In a recent review, West (1982) logically refuted the stereotype concept that salt desert shrubs exist in spatial harmony in equilibrium with the very limited environmental potential of their environment. In fact, chenopod shrubs tend to be grouped in competitive clumps where litter-fall on coppice mounds has enhanced the potential of seedbeds to support germination and seedling establishment (Charley and West 1975). The chance recruitment of seedlings into these communities may be conditioned by erratically occurring episodic climatic events (West 1979).

Due to the lack of atmospheric precipitation and subsequent runoff water, many of the lower pluvial lake basin environments appear remarkably stable once the soil surface becomes stabilized by vegetation and desert pavement formed by wind erosion. We propose that much of this apparent stability is as much a mirage as the genetic stability of the shrub populations. The pluvial lakes shaped the basin bottoms with currents and waves. Sedimentations in the deep water areas were usually very fine textured. Lowering the water level in the lakes lowered the base level of the attendant streams. Landforms and hydrologic processes in and surrounding pluvial lake basins are striving toward stability in a radically different environment. Our purpose was to characterize the major plant communities of a pluvial lake basin in relation to landforms and soils.

METHODS

The study was conducted in Grass Valley, Nevada, 39°52′ latitude, 116°37′ longitude. Grass Valley is a closed basin with a watershed basin of 1,500 km^2. During the Pleistocene, the basin contained pluvial Lake Gilbert, which had a surface area of 400 km^2 (Mifflin and Wheat 1979). The maximum level of Lake Gilbert was 1,766 m. The bottom of the basin is now 1,728 m. Some authorities (e.g., Hubbs and Miller 1945) consider that Lake Gilbert overflowed at its maximum level and formed part of the Lake Lahontan systems. Mifflin and Wheat (1979) point out that the maximum beach ridge of Lake Gilbert is 39 m below the supposed outlet pass.

Color infrared aerial photographs, scale 1:15840, were used for identifying landforms and drainage patterns; plant communities were mapped on 1:62500 U.S. Geological Survey maps. Shrub vegetation in each community was sampled with 10 plots, each 10 m^2 in area. The plots were randomly located along paced transects from a starting point selected on the aerial photographs. The projected crown cover, height, and density of shrubs were recorded by species. The herbaceous vegetation and cryptogamic soil crust (Anderson 1978) were sampled for frequency and cover with four replications of 100 step points using the procedures described by Evans and Love (1957).

Soil profiles were excavated in each major vegetation assemblage. Profiles were described according to the Soil Survey Manual (Anonymous 1951). Soils were classified according to the U.S. Soil Conservation Service system (Anonymous 1975). Soil samples were analyzed for percent gravel by straining through a 2-mm screen; percent sand, silt, and clay were determined using the Bouyocus (1962) method. Electrical conductivity of the saturated soil paste extract was determined by a conductivity meter (Black 1965).

In 1981 a network of shallow wells was installed in three transects from the alluvial fans across the lake plain to the central playa. The wells were distributed along the transects on the basis of plant communities and landforms. The wells were drilled to 4.6 m, with a 10-cm rotary drill and cased with perforated plastic pipe 3.75 cm in diameter, and gravel was packed around the casing. The depth of the water table was measured periodically, and samples were collected and analyzed for electrical conductivity and temperature. A portable signal-enhanced seismograph was used

TABLE 1. Landforms, vegetation, soil texture, percentage of total area, and number of stands sampled for the land area below the maximum level of pluvial Lake Gilbert, Grass Valley, Nevada. Map units refer to Figure 1.

Landform Major subunit	Map unit	Vegetation Dominant species	Soil texture	Area ha	Percentage of total	Number of stands
PLAYA						
Playa	1	None	Clay	6040	15.0	64
Wet depression	1a	None	Clay	10	—	3
Hummocks	1b	*Allenrolfoa occidentalis*	Silty clay loam	10	—	3
Mobile dunes	2	*Sarcobatus vermiculatus*	Clay	120	0.3	12
Haystack dunes	2a	*Sarcobatus* vermiculatus	Clay	10	—	6
Recent Holocene beach	2b	*Kochia americana*	Clay	10	—	2
				6200	15.4	
LAKE PLAIN						
Older Holocene beach	3	*Sarcobatus vermiculatus*	Silty clay loam	2660	7.0	3
Stable dunes	4	*Sarcobatus vermiculatus*	Silt loam	160	0.4	3
Clay dunes	5	*Sarcobatus vermiculatus*	Clay	380	0.9	11
Dune basins	6	*Distichlis/Sporobolus*	Clay	50	1.4	2
Lake plain	7	*Chrysothamnus-Sarcobatus-Artemisia/Elymus*	Silty clay loam	2130	5.3	17
	8	*Sarcobatus/Distichlis*	Silty clay loam	90	0.2	5
	9	*Sarcobatus-Atriplex confertifolia*	Silty clay loam	2160	5.4	7
	10	*Chrysothamnus albidus/Puccinella*	Silty clay	10	—	3
	11	*Atriplex nuttalii*	Silty clay loam	30	0.1	3
				8070	20.2	
Thermal springs	12	*Distichlis/Juncas*	Clay	460	1.1	2
Barrier beach	13	*Sarcobatus vermiculatus*	Clay	820	2.0	2
	14	*Sarcobatus/Kochia*	Clay loam	190	0.5	2
	15	*Atriplex confertifolia*	Silty clay loam	116	0.3	2
				1120	2.8	
Lagoon	16	*Allenrolfea occidentalis*	Clay	1470	3.7	4
	17	*Chrysothamnus nauseosus/Distichlis*	Silty clay loam	990	2.5	3
				2460	6.2	
Sand dunes	18	*Tetradymia/Grayia*	Sand	130	0.3	2
Alluvial fans	19	*Artemisia tridentata*	Loam to gravelly sandy loam	7350	18.3	12
	20	*Atriplex confertifolia*	Silty clay loam to gravelly sandy loam	13760	34.3	21
				21110	52.6	
Bars	21	*Atriplex confertifolia*	Gravelly sandy	370	0.9	3
Lagoons (upland)	22	*Sarcobatus vermiculatus*	Silt loam	130	0.3	3
	23	*Atriplex confertifolia*	Silt loam	60	0.2	3
				190	0.5	

in the summer of 1981 to determine depth to the water table at 35 locations in the valley. The seismographic data were calibrated against wells with known water tables.

RESULTS

The area surveyed was approximately 40,110 ha (Table 1). We established a total of 23 map units (Fig. 1, Table 1). Most of these landform-vegetation-soil map units represent ranges in more or less continuous variation caused by several interacting variables. Some divisions are obvious, but others are arbitrary because of the limits of our current knowledge of these environments.

Plant Communities of the Playa

The surface of the Grass Valley playa is usually free of vegetation (Fig. 2). Obviously the salt content of the surface soils of the playa are limiting to plant growth, but occasional prolonged periods of flooding may be the lim-

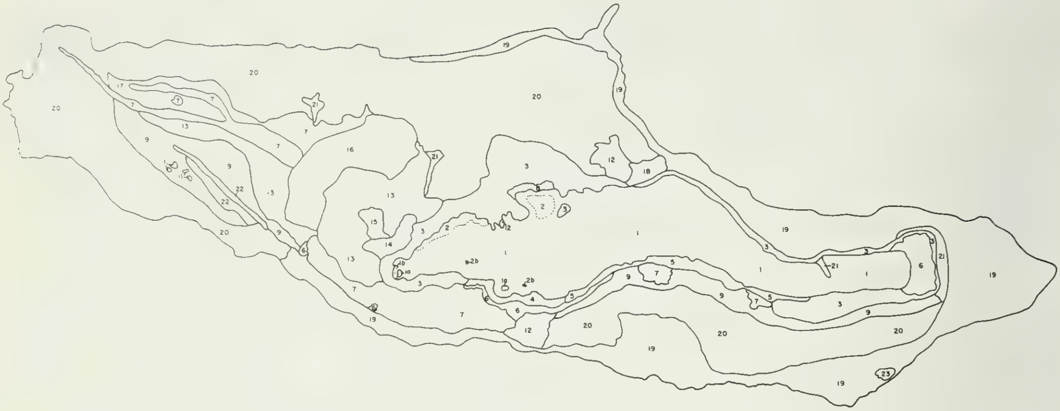
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Fig. 1. Distribution of map units for pluvial Lake Gilbert below the maximum lake level. Units based on landform, soils, and vegetation. *Area* designation (based on dominant plant species) and area of map units given in Table 1.

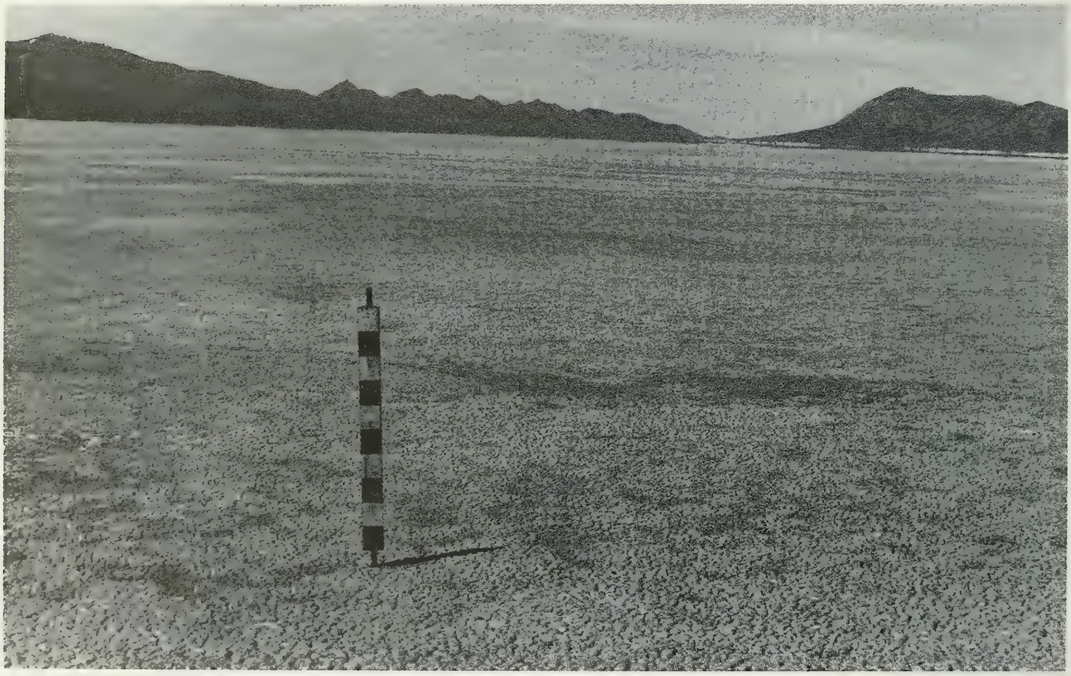

Fig. 2. Grass Valley playas, viewed from a central location looking north. Hot Springs Point (2,300 m), Sawtooth Mountains (2,230 m), Cortez Pass (1,805 m), and Mount Tenabo (2,820 m) on skyline in background from left to right. Note typical polygonal cracking of playa surface. Range pole 1 m divided into dm.

iting factor for the most extreme halophytes. Flooding is probably the factor limiting the spread of rhizomes of the grass *Distichlis spicata* var. *stricta*.[4] Rhizomes, several meters in

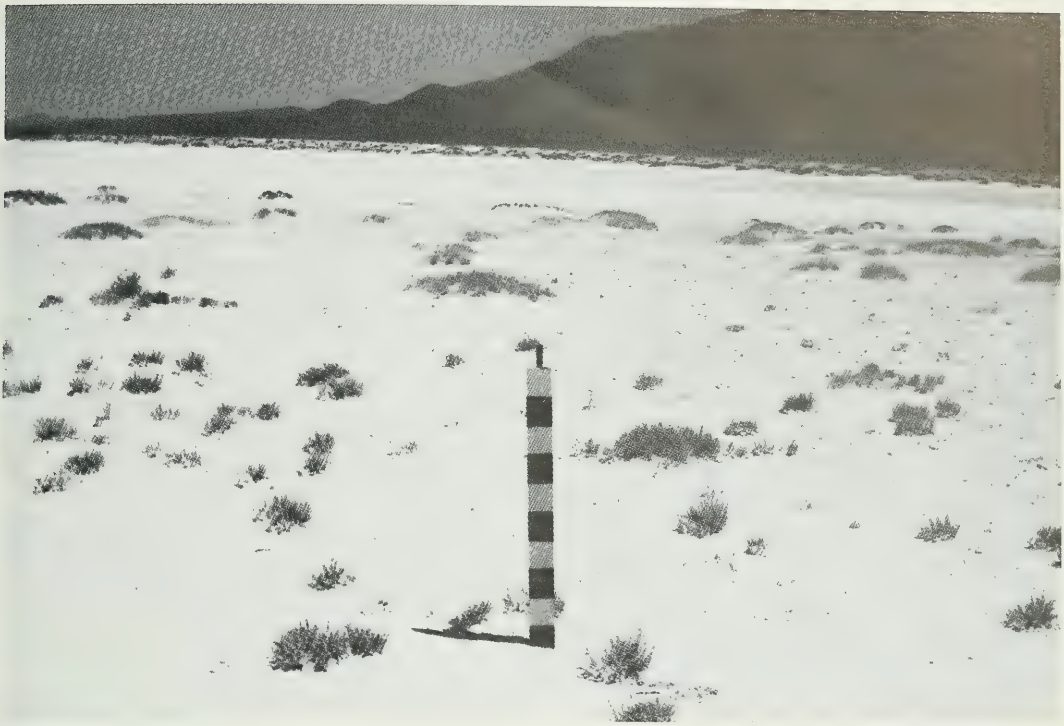

Fig. 3. Wet depressions on margin of playa with effervescence of salt crystals. Middle distance shows group of puff dunes. Holocene beach with scattered plants of *Atriplex nuttalii*. Range pole 1 m divided in dm.

length, can be observed extending down eroded slopes to the playa surface.

Very occasionally, a sparse cover of summer-annual herbaceous vegetation is found on the margin of the playa. *Suaeda occidentalis*, *Atriplex truncata*, and *Halogeton glomeratus* form these communities.

The depth and electrical conductivity of groundwater on the playa varied greatly, depending on the sampling location and season. In the fall, when the playa was dry, the water table in observation wells ranged from 1.5 to 1.8 m below the playa surface. Electrical conductivity of water from the wells ranged from 34 to 105 dS m^{-1}. In the spring, when the groundwater reached the surface of the playa, electrical conductivity of the water dropped to 3 to 10 dS m^{-1}.

Portions of the playa were surveyed and brass plaques were mounted on 3.75–cm–diameter galvanized steel pipe to mark section corners in 1917–1918. By 1979 the pipe supports were faint discolorations in the playa soil profiles. Wooden fence posts planted during the same time period now have bases swollen by salt crystallization to three times their current aerial diameters.

Hummocks.—The wet depressions on the margins are free of vegetation (Fig. 3), but the margins of these depressions are partially ringed with elongated hummocks scarcely 25 cm above the playa surface. The mounds are salt encrusted, and the unwary playa hiker who steps on the mounds for footing in the slimy-slick soils of the wet depression is greeted by a puff of salts that instantly can be tasted. Despite the salinity of the mounds, they are densely vegetated with clumps of *Allenrolfea occidentallis* (Fig. 4). The electrical conductivity of extract from the surface soils of the wet depressions reached values of 400 dS m^{-1} and averaged 34 dS m^{-1}. The texture of the soils of the wet depressions consists of at least two-thirds clay-sized particles, whereas the texture of the mounds is at least two-thirds silt-sized particles.

These mounds may form during drying cycles on the playa when the crystallization of salts around the wet depressions causes miniature salt domes to form. The domes trap

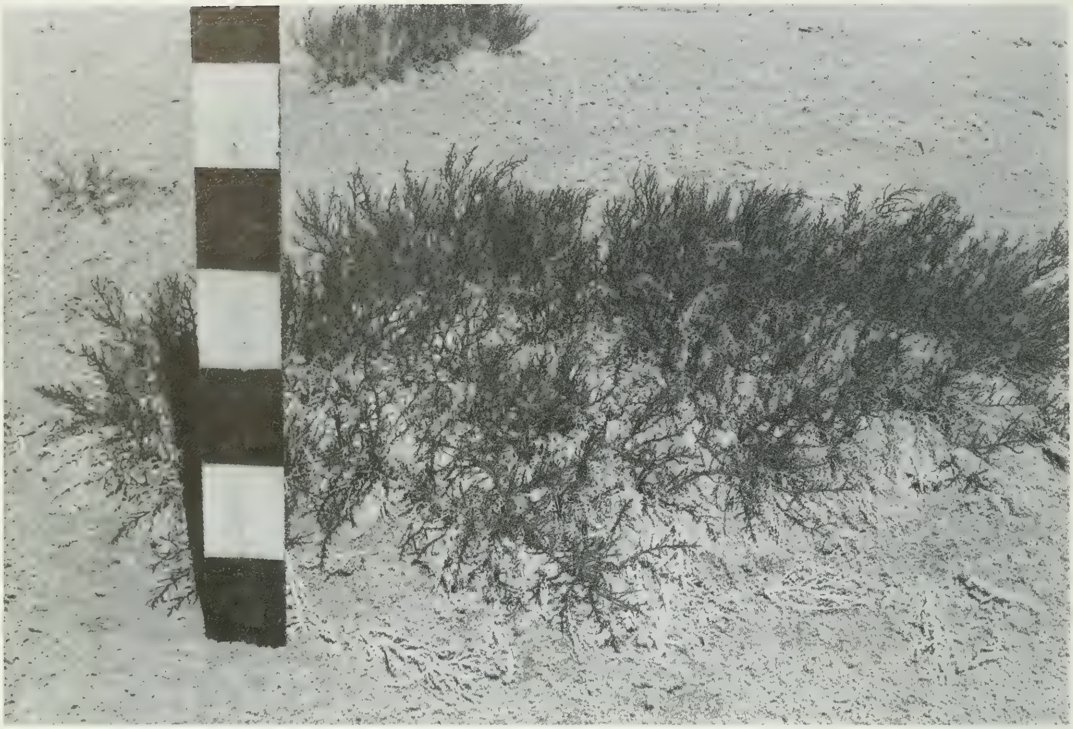

Fig. 4. Small puff dune with *Allenrolfea occidentalis*. Range pole 1 m divided in dm.

silts in their irregular surface topographies and eventually rise high enough above the playa surface to permit the establishment of *Allenrolfea* plants. The silt particles are highly permeable compared to the clays of the playa and therefore may be readily leached of soluble salts.

Mobile Dunes.—Mobile dunes are found on the western margin of the playa, especially where ephemeral streams dump bed loads onto the playa (Fig. 2). These dunes are from 1.0 to 2.0 m in height and are egg shaped in outline (Fig. 5). The pointed end of the dunes is oriented toward the southwest.

The dunes are vegetated with clumps of *Sarcobatus vermiculatus*, a highly variable species. Juvenile plants have a distinct fleshy leaf morphology. Plants growing on upland sites where the groundwater table is not close to the surface are small, stunted, and gray in color. This form is classified as *S. vermiculatus* var. *baileyi*, or it is sometimes raised to the species level (*S. baileyi*).

On the mobile dunes the *Sarcobatus* plants are highly polymorphic. The west-southwest portions of the dunes are usually bare. During dry periods electrical conductivity of the bare soils may reach 250 dS m $^{-1}$. The tops of the dunes are covered with dense patches of dwarfed *Sarcobatus* stems scarcely 2 dm tall. Electrical conductivities of the soils under the dwarf shrubs may reach from 60 to 85 dS m^{1}. The east slopes of the dunes support relatively sparse stands of *Sarcobatus* plants, which reach a meter or more in height. Maximum electrical conductivity of soils on the east slope seldom exceeds from 25 to 40 dS m^{1}. The *Sarcobatus* plants eventually die and the largely clay textured dunes melt away from the skeletons of crowns and roots. Each dune is apparently vegetated with a single clone of *Sarcobatus*.

Haystack Dunes.—Haystack dunes are sparingly distributed along the southeastern margin of the playa, opposite the wave cut escarpment. These dunes range to 7.5 m in height, the tallest being higher than the adjacent lake plain. The east slopes of these large dunes have sparse stands of *Sarcobatus* plants.

Recent Holocene Beach.—This landform is only preserved in discontinuous stretches

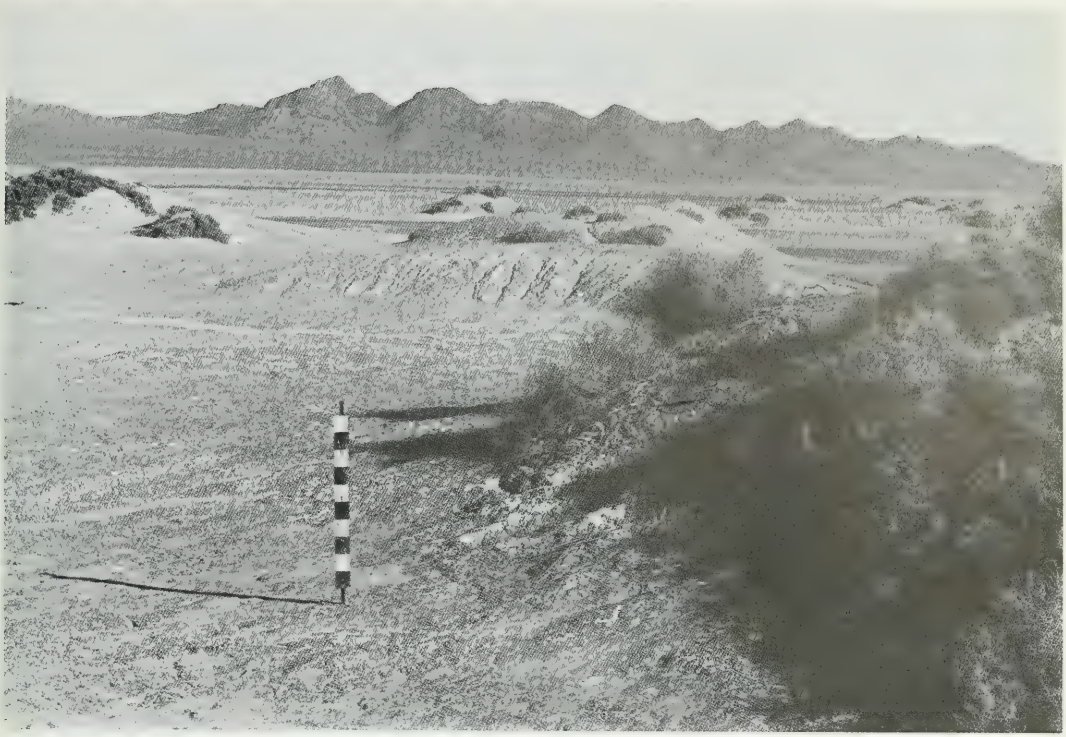

Fig. 5. Mobile dunes vegetated with *Sarcobatus vermiculatus* plants. West side of dunes are largely bare with dwarf plant on top and 1-m tall plants on the east side. If the clones of *Sarcobatus* die, the largely clay-texutred dunes melt away (rilled dune in middle distance) and erode across the playa. Range pole 1 m divided in dm.

around the margins of the playa. It apparently represents some recent rise of the lake of sufficient duration to erode a definite beach into the escarpment of the surrounding lake plain. The discontinuous nature of this beach provides evidence of the highly erodible nature of the interface between playa and lake plain.

Vegetating these fragments of Holocene beach is a relatively dense overstory of shrubs (density 0.9 plants per per m^2, cover 8%) consisting of *S. vermiculatus, Atriplex confertifolia, A. nuttallii,* and *Kochia americana*. Virtually, the only herbaceous species in these communities is *Thelypodium flexuosum*.

Plant Communities of the Lake Plain

Older Holocene Beach.—This is the largest mapping unit of the lake plain associated landforms, constituting 7% of the area of the total pluvial lake basin (Table 1). This landform is located about 2 m higher than the recent Holocene beach that incompletely surrounds the current playa. The general topography is nearly flat from a prominent beach ridge located at 1,730 m elevation to the escarpment at the playa edge (Fig. 6). On the southeast margin of the playa, stable dunes cover the older Holocene beach, and on the northeast side of the playa, clay dunes interrupt drainage to the playa, forming dune basins on the older Holocene beach surface. Occasional drainage channels have eroded channels into the lake plain, creating miniature badland topographies. The microtopography consists of coppice dunes occurring around shrubs and averaging from 20 to 30 cm in height. The coppice dunes support thin, ragged-edge microphytic crusts. The interspace between shrubs is usually bare of vegetation and microphytes.

Soils of the lake plain largely belong to the order Inceptisols (Anonymous 1975). A typical soil for the older Holocene beach would be classified as a fine, montmorillonitic (calcareous), mesic Aeric Halaquept. A typical profile consists of a dark, grayish brown salt- and sodium-affected silty clay surface horizon, over a thick (2 m) light gray lacustrine clay

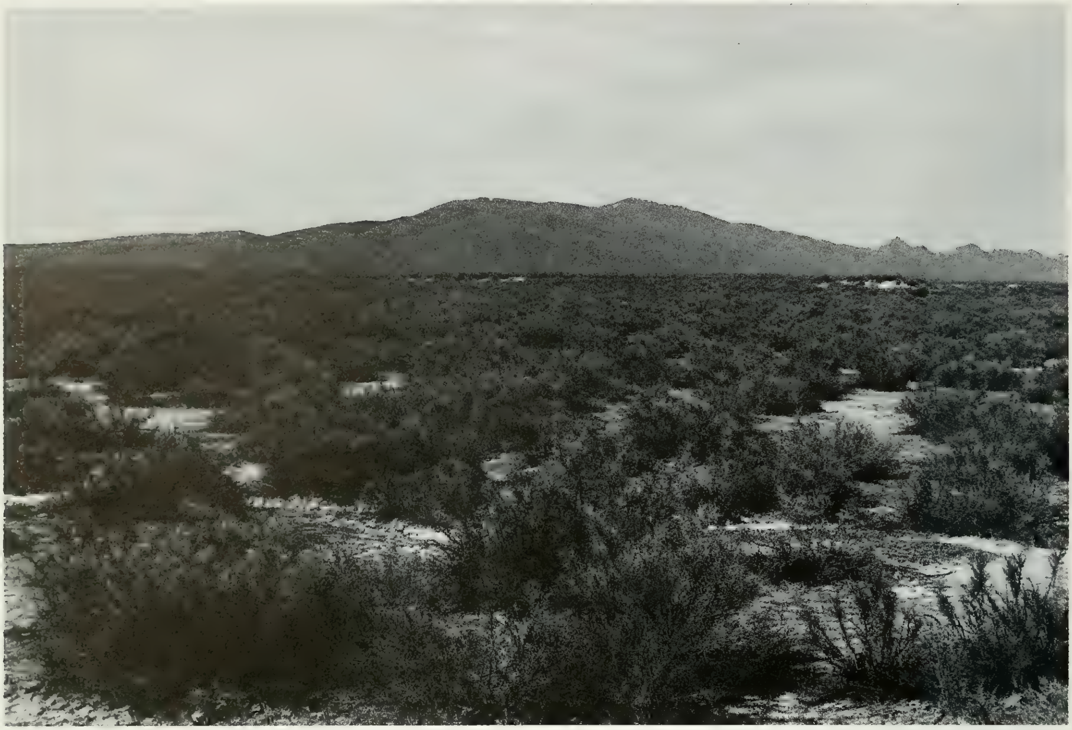

Fig. 6. *Sarcobatus vermiculatus*-dominated plant community located on older Holocene beach on lake plain.

horizon. Below this layer iron mottles are common. Sodium absorption ratios of these soils are 45 or greater, with average electrical conductivity of the saturation extract of 8 to 12 dS m^1. In the upper 30 cm, the predominant salts are sodium chloride and sodium sulfate (Roundy 1984). Salt concentrations of the surface soil decrease due to leaching by winter and spring precipitation and increase with the lack of precipitation in the summer (Roundy et al. 1983).

The depth of the water table on the older Holocene beaches averages 3.2 m during dry periods and 2.1 m in the spring. However, the amount of variation measured was highly dependent on location. Apparently the nature of the watershed and alluvial fan at the mouth of the watershed influences the groundwater on the lake plain adjacent to the alluvial fan. Snowmelt in surrounding mountains causes ephemeral streams to flow on the mountain escarpment in May and early June. As the water leaves the pediment surface, it disappears on the relatively coarse alluvial fans. The water moving down through the fans apparently strikes buried, fine-textured lacustrine deposits from previous high rises of the lake. Lateral movement of groundwater occurs with discharge in springs or seeps where past wave action has truncated alluvial fans. There is a delay of a month to six weeks between the water disappearing at the mouths of canyons along the mountain escarpment and rising groundwater levels on the lake plain. Below some alluvial fans, even if they were deposited at the mouths of large watersheds, the groundwater level on the lake plain does not vary.

Similar relationships were apparent for soluble salt content of the groundwater. In areas where the water table varied, electrical conductivity of water from the wells dropped as the water table rose and increased as the water table dropped. Where the water table remained stationary, electrical conductivity of the water was very constant.

The plant communities of the older Holocene beach are dominated by *Sarcobatus vermiculatus* shrubs with varying amounts of *Atriplex confertifolia* (Fig. 3). Cover of both species of shrubs was only 12% (Table 2). Only six herbaceous species were recorded in the understory (Table 3). A Cruciferae, *Thelypodium flexuosum*, was the most frequent herbaceous species encountered.

Atriplex confertifolia tended to occur in relatively pure stands within a matrix of *S. vermiculatus*. The *A. confertifolia*-dominated areas had deeper water tables. *Sarcobatus vermiculatus* is a pronounced phreatophyte with reported rooting to water tables at depths of 7.5 m (White 1932). However, the very low permeability of the clay soils, coupled with the scant atmospheric precipitation associated with the central basin locations, may never result in soil wetting to the water table to permit contact of *S. vermiculatus* roots with the groundwater fringe.

Stable Dunes.—Floristically and physiognomically, the plant communities of the stable dunes are very similar to those of the older Holocene beach. The soil of the stable dunes is classified as a coarse-silty, mixed (calcareous), mesic, Aquic Durorthidic Torriorthent of the order Entisol. The soils are very deep and moderately well drained because of the relatively coarse texture. Typically the surface layer is light gray silt. The underlying material to a depth of 2 m is light brownish gray and light gray stratified and very fine sandy loam and silt loam with discontinuous weak silicon concentration in the upper part. Despite the quite different soil and a generally greater depth to the groundwater table, only the shrub *Grayia spinosa* was added to the plant communities of the stable dunes compared to the older Holocene beaches of the lake plain (Table 2).

Clay Dunes.—With only 8% plant cover, there is little vegetation on the clay dunes (Table 2 and 3). The microdrainages and valleys among the dunes are occupied by flows of salt crystals that are apparent after a rain. Vegetation is generally restricted to the top and east side of the dunes.

Dune Basins.—The dunes, either stabilized or clay, interrupt drainage from the lake plain to the playa. In wet years ephemeral lakes form in the basins (Fig. 7). The typical soils of these basins are classified as fine silty, mixed (calcareous) mesic Aeric Fluvaquents. These soils range from slightly to strongly saline. The slightly saline soils are in the lowest depressions that are subject to spring ponding. The soils are very deep and poorly drained. Typically the surface layer is light gray, strongly salt- and sodium-affected clay loam.

Sampling the observation wells indicated that the water table depth under this landform ranges from 0.5 to 1.0 m below the soil surface. The electrical conductivity of the water ranged from 0.8 to 1.0 dS m^{-1}.

Repeated flooding limited shrubs in the dune basin community to occasional plants of *Chrysothamnus nauseosus* ssp. *consimilis*, but a total of 27 herbaceous species was recorded in the basins (Tables 2 and 3). *Distichlis spicata* var. *stricta* was the most frequent herbaceous species.

Lake Plain.—The lake plain itself accounts for more than 10% of the basin below the maximum level of the pluvial lake basin. Generally the lake plain is physically positioned above the offshore bar that forms the upper boundary of the older Holocene beach (1,730 m elevation) and a prominent beach that truncates alluvial fans at 1,740 m elevation. The elevations are from the top of one bar to the top of the other bar. Once the plunge pit behind the bottom bar is passed, the lake plain is nearly flat until the 1,740 m bar is reached. The lake plain is not distributed symmetrically in the basin (Fig. 1). Most of the lake plain is located between the southeastern margin of the playa and the wave-truncated alluvial fans at the base of the mountain escarpment. On the northwest margin of the playa, the playa extends to the alluvial fans with no lake plain.

The genesis of the soils of the lake plain apparently combines: (a) periods of relatively deep water flooding with deposition of fine-textured lacustrine sediments; (b) recurring periods of lake desiccation with aeolian erosion and deposition, coupled with alluvial fan encroachment onto the plain; and (c) recurrent flooding with truncation of the alluvial fans and subsequent incorporation of alluvial material into the lacustrine sediment by wave and current action.

Such complex soil formation factors produce a range of soil morphologies depending on the volume of material, the physical and chemical nature of the inputs from alluvial fans, and the physical position in the pluvial lake basin. A typical soil for the bulk of the lake plain above the older Holocene beach

TABLE 2. Density per m^2 and projected cover of shrub species in plant communities (mapping unit number) of the lake plain and associated landforms.

	Landform, plant community, density, and cover							
	Older Holocene beach (3) *Sarcobatus vermiculatus*		Stable dunes (4) *Sarcobatus vermiculatus*		Parma dunes (5) *Sarcobatus vermiculatus*		Dune basins (6) *Distichlis-Sporobolus*	
	Density per m^2	Cover %	Density per m^2	Cover %	Density per m^2	Cover %	Density per m^2	Cover %
CHENOPODIACEAE								
Atriplex confertifolia	0.2	2.0						
Grayia spinosa			.1	0.2				
Sarcobatus vermiculatus	0.8	10.0	1.1	14.0	0.6	4.0		
COMPOSITAE								
Artemisia tridentata ssp. *tridentata*								
Chrysothamnus nauseosis ssp. *consimilis*							0.3	0.2
Chrysothamnus albidus								
Totals	1.0	12.0	1.2	14.2	0.6	4.0	0.3	2.0

TABLE 3. Frequency (%) and total cover of herbaceous species in plant communities (mapping unit numbers) of the lake plain and associated landforms.*

	Older Holocene beach (3) *Sarcobatus vermiculatus*		Stable dunes (4) *Sarcobatus vermiculatus*		Parma dunes (5) *Sarcobatus vermiculatus*		Dune basins (6) *Distichlis - Sporebolus*	
	Frequency %	Cover %	Frequency %	Cover %	Frequency %	Cover %	Frequency %	Cover %
CAPRIFOLIACEAE								
Cleonella plocusperma							1	
CHENOPODIACEAE								
Atriplex truncata	2						2	
Halogeton glomeratus	2		2					
Monolepis nuttalliana							T	
Nitrophilia occidentalis							3	
Salsola iberica	4							
COMPOSITAE								
Aster occidentalis							T	
Crepis runcinata							2	
Haplopappus lanceolatus							T	
Haplopappus uniflorus							1	
Hymenoxys lemmonii							1	
Solidago spectabilis							T	
Taraxacum officinale							T	
CRUCIFERAE								
Capsella bursa-pastoris								
Descurinia sophia								
Lepidium perforiatum	4		2				6	
Thelypodium sagittatum							T	
Thelypodium flexuosum	86		92		54			
GRAMINAEAE								
Distichlis spicata var. *stricta*	2		4		46		54	
Elymus cinereus							3	
Elymus triticoides							1	
Hordeum pusillum							1	
Muhlenbergia rohardsonis							2	
Puccinellia airoides							5	
Puccinellia lemmonii							2	
Sitanion hystrix								
Spartina gracilis							T	
Sporobolus airoides							8	
JUNCAGINACEAE								
Triglochin maritina							1	
PLANTAGINACEAE								
Plantago eripoda							1	
ROSACEAE								
Potentilla anserina							1	
Potentilla pectinisecta							4	
Ivesia kingii							2	
	7		9		4		86	

Lake plain									
Chrysothamnus-sarcobatus/ Artemisia-Elymus (7)		*Sarcobatus/ Distichlis* (8)		*Sarcobatus/Atriples* (9)		*Chrysothamnus*/(10) *Puccinella*		*Distichlis* (11)	
Density per m^2	Cover %	Density per m^2	Cover %	Density per m^2	Cover %	Density per m^2	Cover %	Density per m^2	Cover %
				1.1	9.2				
0.2	2.0	1.0	16.0	.6	3.0				
1.0	15.1								
.4	4.0	0.2	3.0					0.3	3.0
						0.4	3.0		
1.6	21.1	1.2	19.0	1.7	12.2	0.4	3.0	0.3	3.0

Lake plain									
Chrysothamnus-Sarcobatus-(7) *Artemisia/Elymus*		*Sarcobatus*/(8) *Distichlis*		*Sarcobatus*-(9) *Atriplex*		*Chrysothamnus*/(10) *Puccinella*		*Distichlis* (11)	
Frequency %	Cover	Frequency %	Cover	Frequency %	Cover	Frequency %	Cover	Frequency %	Cover
T									
T		2							
T				5					
		1				2		1	
T									
								T	
						2		3	
								T	
						4		T	
								1	
								T	
1									
3				6					
8		85				8		77	
72								2	
								1	
		2				36			
						48		12	
16									
								T	
								1	
								2	
								T	
16		49		6		11		74	

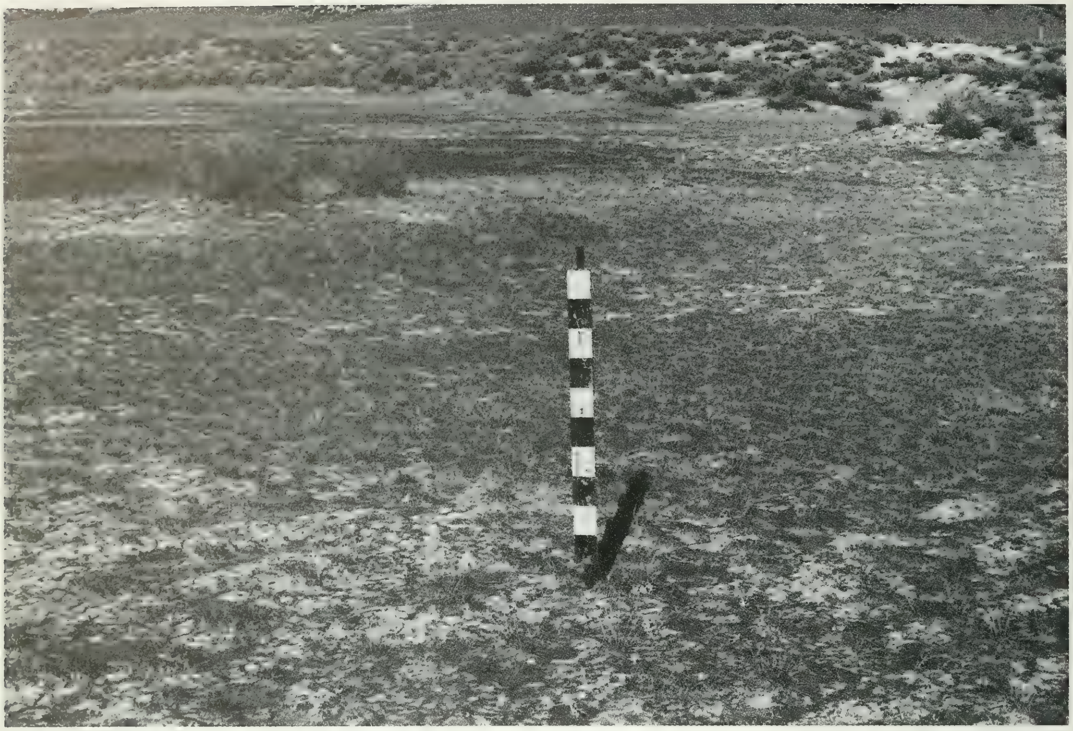

Fig. 7. Dune basin with fairly dense ground cover of *Distichlis spicata* var. *stricta*. In background stabilized dunes with *Sarcobatus vermiculatus* shrubs.

would be classified as a mixed (calcareous), mesic family of Aquic Durorthidic Torriorthent. Typically the surface horizon is pale brown and sodium-affected (sodium absorption ratio >40) silt loam about 10 cm thick. The upper 50 cm of the underlying material is pale brown silt loam that is weakly silicon-concentrated in the lower part. This horizon rests upon at least 2 m of light gray to yellow clay.

The above soil is associated with a complex plant community that combines as dominant species *Artemisia tridentata* ssp. *tridentata*, *Chrysothamnus nauseosus* ssp. *consimilis*, *Sarcobatus vermiculatus/Elymus cinereus* (Tables 2 and 3, Fig. 8). This is a plant community that should not exist because the autecology of the woody dominants is in apparent opposition to each other. *Artemesia tridentata* ssp. *tridentata* is probably the most highly evolved taxon of the *A. tridentata* polyploid complex that characterizes the landscape above the maximum level of pluvial lakes in the Great Basin (McArthur and Plummer 1978). It is not considered to be a salt-tolerant species. *Chrysothamnus nauseosus* ssp. *consimilis* is a morphologically distinct subspecies in a complex group of root-sprouting shrubs (McArthur et al. 1978). The subspecies *consimilis* is the only *Chrysothamnus* of the *nauseosus* group that is found in abundance in saline/alkaline habitats (Roundy et al. 1981). *Sarcobatus vermiculatus* is not competitive in upland nonsaline/alkaline situations, and the soluble salt residue from *S. vermiculatus* litter has been demonstrated to increase the salinity of the surface to the point of excluding reproduction of *A. tridentata* (Rickard 1965).

The distribution of the dominant shrubs is highly variable, with occasional patches containing an equal representation of these three species. Essentially, *S. vermiculatus* and *A. tridentata* represent saline and nonsaline soil extremes, respectively, with *C. nauseosus* ssp. *consimilis* being more or less able to compete in both extremes as long as the water table is relatively shallow. The swirling, apparently meaningless patterns of distribution of the three dominant shrub species in this environment apparently reflect equally complex evolution of salinization-desalination of the older lake plain soils.

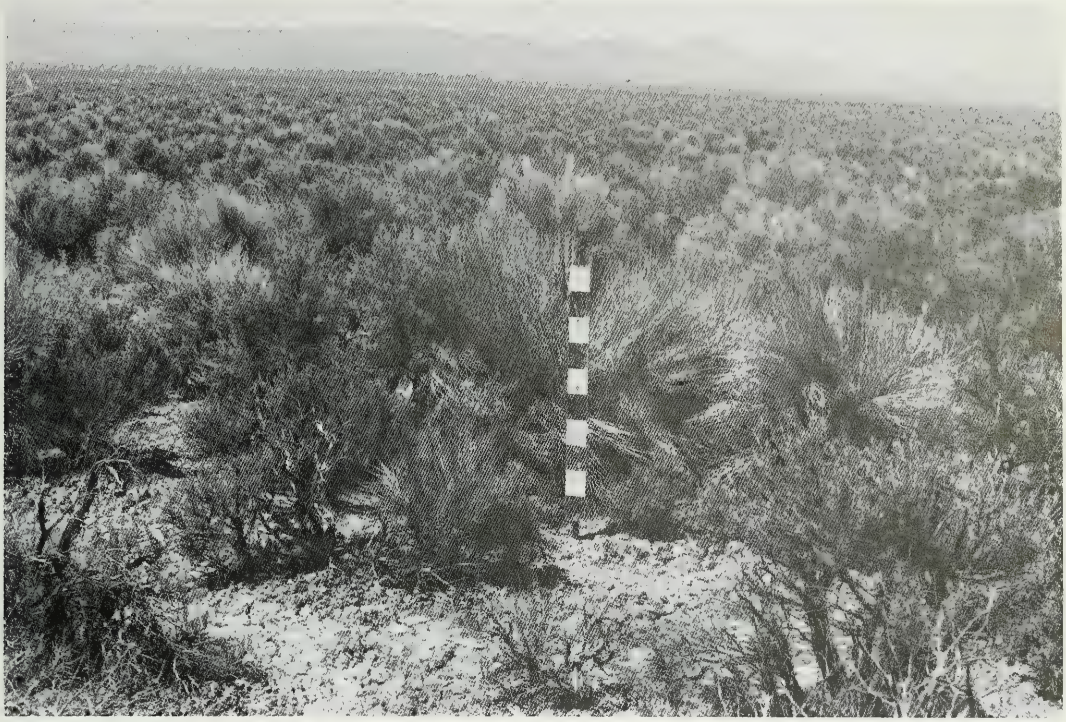

Fig. 8. Most abundant plant community on the older lake plain landforms. Overstory dominants *Artemisia tridentata* ssp. *tridentata*, *Chrysothamnus nauseosus* ssp. *consimilis*, *Sarcobatus vermiculatus*. Understory dominant, which was the mammoth, tufted perennial grass *Elymus cinereus*, is now much depleted by grazing of domestic livestock.

The herbaceous dominant, *Elymus cinereus*, has been greatly depleted by past excessive grazing of domestic livestock (Lesperance et al. 1978). Under pristine conditions, in particularly favorable locations for soil moisture on the lake plain, the annual biomass production of this grass probably reached 2000 kg/ha.

The *Sarcobatus-Atriplex*-dominated plant communities of the older lake plain are similar in appearance and structure to those found on the older Holocene beach (Tables 2 and 3). These xeric communities are associated with areas with deeper water tables that do not fluctuate seasonally.

On the mesic end of the spectrum, several communities exist where the groundwater reaches the soil surface at least sometime during the growing season. In *Chrysothamnus albidus/Puccinella* species, the perennial grasses occur on miniature pedicels. The *Distichlis* meadows are wet to the soil surface relatively late in the season, when water percolating through the alluvial fans comes to the surface on the lake plain. This coincides with the phenology of *Distichlis* for summer growth.

In the high water table portion of the lake plain, the soluble salts in the soil profile are largely concentrated on the soil surface by capillary discharge of groundwater.

Located on the far southern extremes of the lake plain are several islands of vegetation completely dominated by *Atriplex nuttallii*. Only a few plants of *Kochia americana* share the communities. The heavily grazed *A. nuttalli* plants are under 10 cm high, so the communities stand out sharply from the 1-m tall mixed shrubs of the surrounding lake plain communities. Other than the very regular lower contact boundary of the soil horizons beneath the *A. nuttallii* communities, there are no obvious soil differences between the *A. nuttallii* islands and the surrounding vegetation.

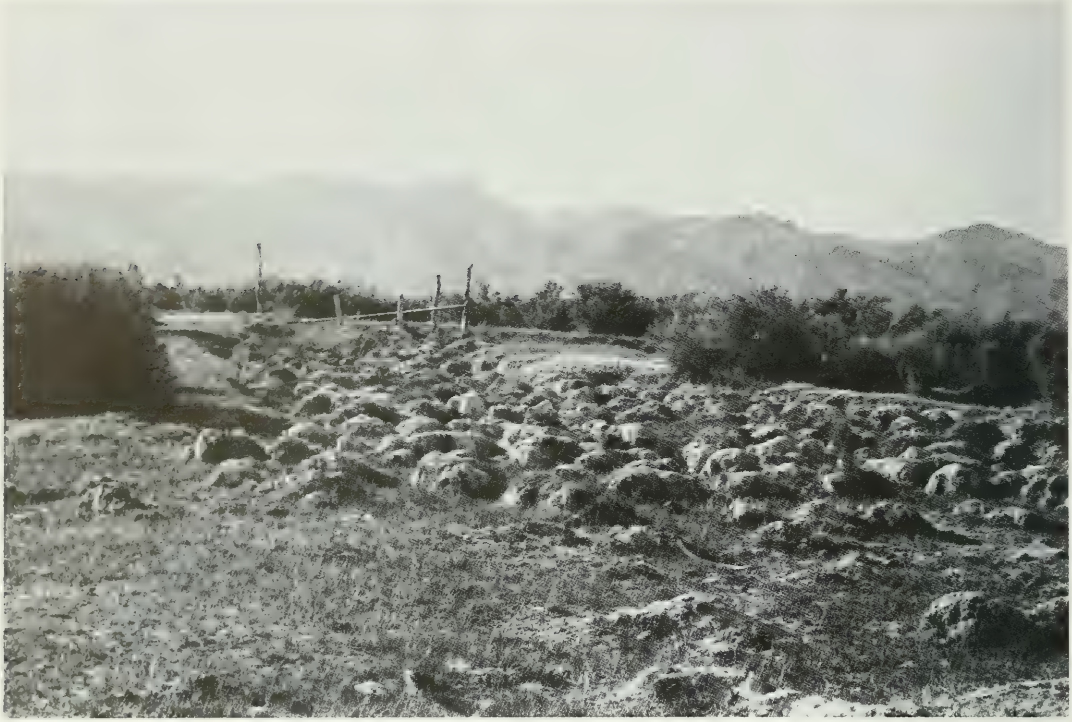

Fig. 9. Little Hot Springs, Grass Valley, Nevada. Springs support a few square meters of saline/alkaline meadow surrounded by *Sarcobatus vermiculatus* plants located on a peninsula in the center of the playa. The Little Hot Springs is the only source of water for a large area. Mounds were caused by cattle trampling in mud trying to drink. Poles have been placed in caldera of hot springs to discourage cattle from entering.

Thermal Springs

There are three groups of thermal springs below the maximum level of pluvial Lake Gilbert (Fig. 1, map unit 12). The largest group of springs, the Walti Hot Springs, are on the east central edge of the valley near the maximum level of the lake. The flora around these hot springs has been highly disturbed by agricultural activities, but the occurrence of species such as *Spartina gracilis*, *Juncus balticus*, and the central Nevada endemic *J. longistylis* suggests what the vegetation composition of the shoreline may have been around pluvial Lake Gilbert.

The Little Hot Springs, located in the center of the playa, support only a few square meters of *Juncus-Distichlis* meadow (Fig. 9). Hot Springs Point on the west side of the playa has several thermal springs on large mounds of tufa. Runoff from these springs supports *Distichlis* meadows.

Initially we did not take the temperature of groundwater in the wells when water samples were obtained. In the second year of sampling, when temperatures were taken, it was determined that on the same day the temperature of the surface of the water table varied by more than 20 C among wells. We considered none of the wells to be located in the thermal springs areas, but slightly geothermal groundwater is widespread on the lake plain.

The almost complete lack of tufa deposits in the basins of pluvial Lake Gilbert is noteworthy considering the thick mantles of tufa deposited in Lake Lahontan (Morrison 1969). The hot springs should have built tufa domes if they were active during the pluvial lake period (Papke 1976).

Plant Communities of Barrier Bar and Lagoon

In the central part of the Valley, south of the playa, extensive areas of *Sarcobatus vermiculatus* communities were delineated. Some of these communities supported cryptogamic crusts in the interspaces between shrubs and stands of *Kochia americana*, which is highly

TABLE 4. Density per m^2 and projected cover of shrub species in plant communities on the barrier bar and lagoon.

	Barrier beach						Lagoon			
	Sarcobatus vermiculatus		*Atriplex confertifooia*		*Sarcobatus-Kochia americana*		*Allenrolfea occidentalis*		*Chrysothamnus nauseosus ssp. consimilis/Distichlis*	
	Density m^2	Total cover %	Density m^2	Total cover %	Density m^2	Total cover %	Density m^2	Total cover %	Density m^2	Total cover %
CHENOPODIACEAE										
Allenrolfoa occidentalis							0.4	5.2		
Atriplex confertifolia	.2	3.0	1.3	8.0						
Kochia americana					1.8	2.0				
Sarcobatus vermiculatus	.9	11.0	.8	4.3	1.2	16.0	0.2	3.1	0.2	0.4
COMPOSITAE										
Artemisia tridentata ssp. *tridentata*		T								
Chrysothamnus nauseosus ssp. *consimilis*		T							0.8	8.4
Totals	1.1	14.0	2.1	12.3	3.0	18.0	0.6	8.3	1.0	8.8

TABLE 5. Frequency (%) and total cover of herbaceous species on the barrier bar and lagoon landforms.

	Barrier beach						Lagoon			
	Sarcobatus vermiculatus		*Atriplex confertifolia*		*Sarcobatus-Kochia americana*		*Allenrolfea occidentalis*		*Chrysothamnus nauseosus ssp. consimilis/Distichlis*	
	Frequency %	Total cover	Frequency %	Total cover	Frequency %	Total cover	Frequency %	Total cover	Frequency %	Total cover
CAPRIFOLIACEAE										
Cleomella plocasperma	2	T	6	T	2	T				
CHENOPODIACEAE										
Atriplex truncata					6	1				
CRUCIFERAE										
Thelypodium flexuosum	92	2	94	2	88	3				
GRAMINAEAE										
Distichlis spicata var. stricta	6	T			4	T	100	8	100	38
Elymus cinereus										
		2		2		3		8		38

preferred by domestic livestock. We at first assumed the communities represented a higher level of range condition than was previously observed on similar soils on the older Holocene beach. Distance from water would have limited grazing in these central valley communities (Stewart et al. 1940). A map produced from satellite data showed this area as a separate unit from the remaining lake plain (unpublished data, P. T. Tueller, Division of Range, Wildlife, and Forestry, University of Nevada, Reno). Further investigations revealed a large depression to the south (up watershed). This depression contained reddish colored dunes composed of clay and salt particles. The vegetation on these dunes was almost entirely *Allenrolfea occidentalis*, an extremely salt-tolerant chenopod.

We delineated a large rectangular island about 3.3 by 5 km stretching across the valley from the older lake plain on the east to a 2.5-km-long gravel bar on the west side of the valley. On the north and south sides of the island, escarpments of about 4.5-m height existed. Callaghan Creek was incised into the island with a multiterrace cut about 4.5 m deep. Cowboy Rest Creek incised a channel along the west boundary of the island before continuing on to the playa. We theorized that the island was a result of isostatic rebound following the evaporation of the waters of pluvial Lake Gilbert. Isostatic rebound has been noted for the deeper parts of Lake Lahontan (Mifflin and Wheat 1979). Closer examination suggested that waves driven by northerly winds on the long axis of the valley built a

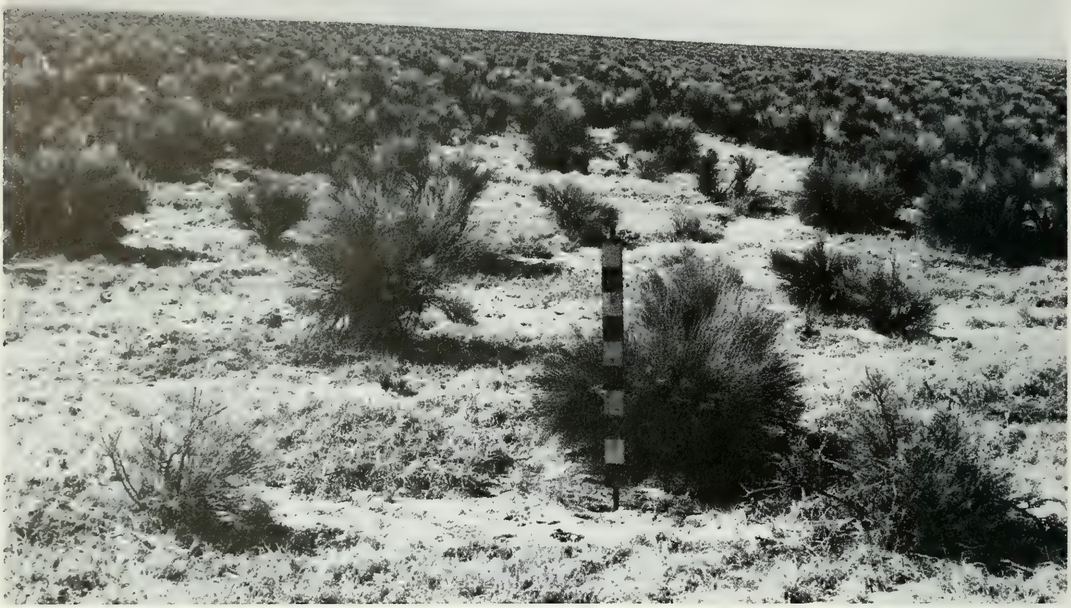

Fig. 10. *Chrysothamnus nauseosus* ssp. *consimilis*/*Distichlis spicata* var. *stricta* plant communities on the south maring of the *Allenrolfea* dunes in the eroded lagoon. Range poles 1 m divided in dm.

barrier bar across the south end of the basin. A similar bar, on a much smaller scale, is being built across the northern end of the present playa. A third barrier bar may have been built upstream on Callaghan Creek extending out from the most southerly gravel bar (Fig. 1). The only inconsistency with the barrier bar hypothesis for the origin of the central island landform is the lack of a gravel veneer on the bar. The lack of gravel may have been the result of the deep water location of the bar, or the gravel veneer may be buried by subsequent subaerial deposition on the area.

Whatever the origin of the landform, what we identified as the barrier bar served two functions in the evolution of soils and vegetation assemblages in the central valley area. First, the island is elevated above the surrounding landforms, so no overland flow is received from adjacent landforms. The lack of microdrainage patterns and the well-developed cryptogamic crust on the soil surface indicate a very stable surface landscape. Secondly, the island structure apparently blocked drainage from Callaghan Creek to the central playa, creating a large lagoon. Since the central lake level dropped to the present level of the playa, Callaghan and Cowboy Rest creeks have breached the barrier, allowing erosion of the sediments trapped in the lagoon and the drainage pattern of the entire south end of the valley to erode toward a new base level.

The sediments in the lagoon contain more soluble salts than the surface soils of the present playa. Some soils from the *A. occidentalis* field were 50% soluble salts. Microscopic examination of these soils revealed aggregations of salt crystals that were worn by saltation until well rounded.

The plant communities of the barrier bar and lagoon are characterized by a poverty of species (Tables 4 and 5). South of the *A. occidentalis* dunes in the lagoon area, extensive areas of *C. nauseosus* ssp. *consimilis*/*D. spicata* var. *stricta* plant communities occur (Fig. 10).

Plant Communities of Sand Dunes

Sand-textured soils are very rare in the basin of pluvial Lake Gilbert only 0.3% of the landscape is covered with sand dunes (Table 1). The well-stabilized dunes are located on an older lake plain surface on the west side of the valley. The sands are not salt affected and support a diverse shrub and herbaceous plant community. Besides the shrubs *A. tridentata* and *S. vermiculatus*, the dunes support *Grayia spinosa* and *Tetradymia comosa*. Several herbaceous species such as the grasses *Oryzopsis hymenoides* and *Sitanion hystrix*, which are characteristic members of plant communities found on alluvial fans, were found on the sand dunes.

Plant Communities of the Alluvial Fans

Over half the area below the maximum level of pluvial Lake Gilbert is occupied by alluvial fans spreading out from the mountain escarpment. Most of this area is covered by various plant communities that are dominated by *Atriplex confertifolia*.

In the southern end of the basin, the pluvial lake was very shallow (less than 7.5 m). The lake sediments are mixed with alluvial material. The *Atriplex confertifolia* plants that dominate this area are less than 0.3 m tall, with total projected crown cover of the shrub around 10% (Fig. 11). Mixed with the *A. confertifolia* are *Sarcobatus baileyi* plants. Where the alluvium has mixed with shallow lake sediments, gravel has sorted to the soil surface to form desert pavement in the interspaces among shrubs. The shrubs are growing on small mounds, from 10 to 35 cm above the interspace surfaces.

Several soils are found in the area dominated by *A. confertifolia,* most of which are Aridisols. The oldest landforms support Haplargids soils. These soils have an argillic horizon. Commonly a calcium horizon has been developed below the argillic horizon. Many of the soils on the pluvial lake sediments are Orthids. These soils commonly have horizons of accumulations of soluble salts and carbonates. The soils do not have argillic horizons.

On the west side of the valley, there is an area of *A. confertifolia/Oryzopsis hymenoides* in apparent high seral status, as a result of protection from grazing by distance from water (Table 6). The density of shrubs here is about the same as in the grazed areas, but the shrub interspaces support a good stand of the perennial grass *O. hymenoides*, with the perennial grass *Sitanion hystrix* found under shrub canopies.

The relationship between *Atriplex* and *Artemisia* communities on the alluvial fans is very complex. The most abundant *A. confertifolia* community in the basin consists of a mosaic of *Artemisia tridentata* ssp. *wyomingensis* in the microdrainageways, with the bulk of the intervening residual soil occupied by *A. confertifolia*.

The alluvial fan consists of a series of fans of differing age. On the southeasterly margin of the valley, *A. conferifolia* extends up the alluvial fans to the mountain escarpment without the intervening *Artemisia*-dominated communities. Along the east central margin of the basin, *A. tridentata* ssp. *wyomingensis* communities extend to the lake plain without intervening *A. confertifolia* communities. This distribution may be due to orographic influences on precipitation, both mountains to the east that accumulate precipitation and mountains to the west that cast rain shadows. Where *A. tridentata* and *A. confertifolia* communities abut each other laterally along the alluvial fans, *A. confertifolia* appears to occupy the older alluvial fan.

The plant communities of the alluvial fans dominated by *A. tridentata* ssp. *wyomingensis* have been described in detail by Cluff et al. (1983). The herbaceous vegetation in the understory of the *Artemisia* community is dominated by the alien annual grasss *Bromus tectorum.* Apparently this weed can not tolerate the salt content of the lake plain soils. Ruderal and disturbance weeds in this environment are *Salsola iberica* and *Halogeton glomeratus*.

Plant Communities of Bars

Ranging from the playa to well upon the older lake plain, there are several current bars largely composed of well-sorted gravels. Some of these are 10 km long and rise from the lake plain like railroad embankments (Fig. 12). The typical soils on these bars are Xerollic Camborthids. The most abundant plant communities are dominated by *A. confertifolia/Artemisia spinescens*.

A second form of bars are offshore bars formed between alluvial fans along the margins of the valley. The soils of these bars are similar to those noted for the larger current bars. Wave plunge pits were formed behind these offshore bars. Most of the plunge pits

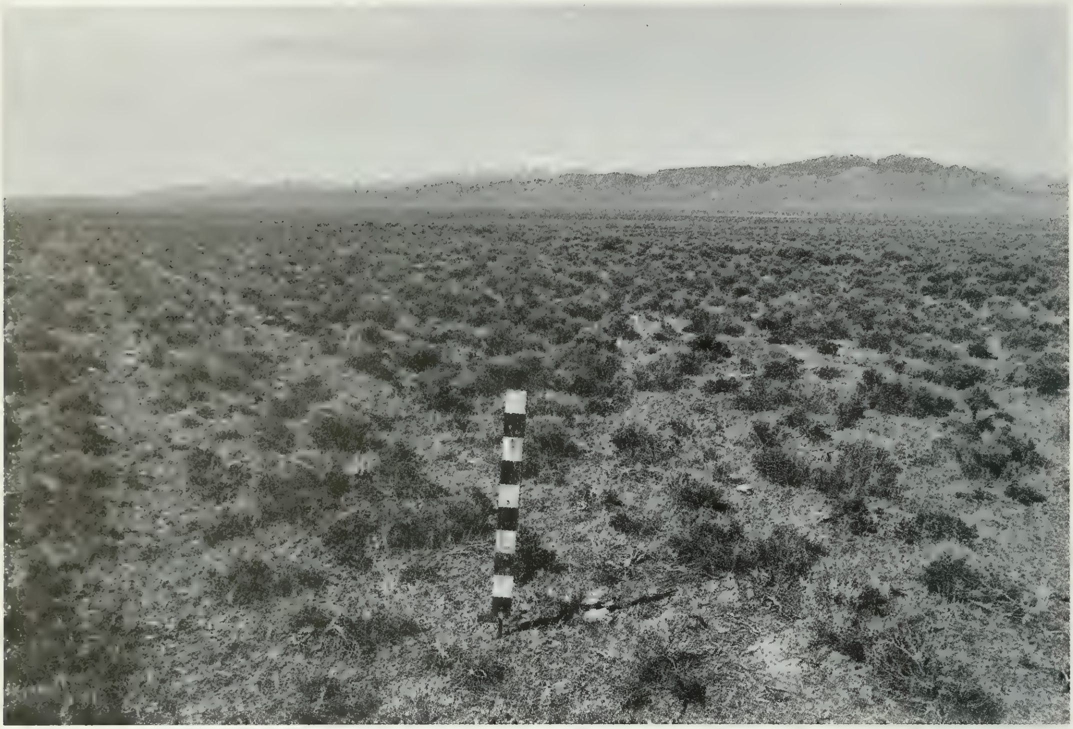

Fig. 11. *Atriplex confertifolia*-dominated communities at the south end of Grass Valley, Nevada. Range pole 1 m divided in dm.

TABLE 6. Density per m^2 and projected cover of shrub and frequency and cover of herbaceous species in a high condition *Atriplex confertifolia/Oryzopsis hymenoides* community.

	Shrub		Herbaceous	
	Density per m^2	Cover %	Frequency %	Total cover
SHRUBS				
Chenopodiaceae				
Atriplex confertifolia	.8	.8		
Sarcobatus baileyii	.2	.2		
Compositae				
Artemisia spinescens	.1	.1		
Total	1.1	11		
HERBACEOUS				
Cruciferae				
Thelypodium flexuosum			9	
Graminaeae				
Sitanion hystrix			27	
Oryzopsis hymenoides			64	
				11

are now filled with silt-textured sediments that are thought to be the result of wind erosion off the playa and subsequent subaerial despoition on the alluvial fans (Young and Evans 1984). The fine-textured deposition material was reeroded to the natural basins of the plunge pits. We called the filled-in plunge pits lagoons.

The soils of the lagoons are Durorthidic Torriorthents. Some of the lagoons support

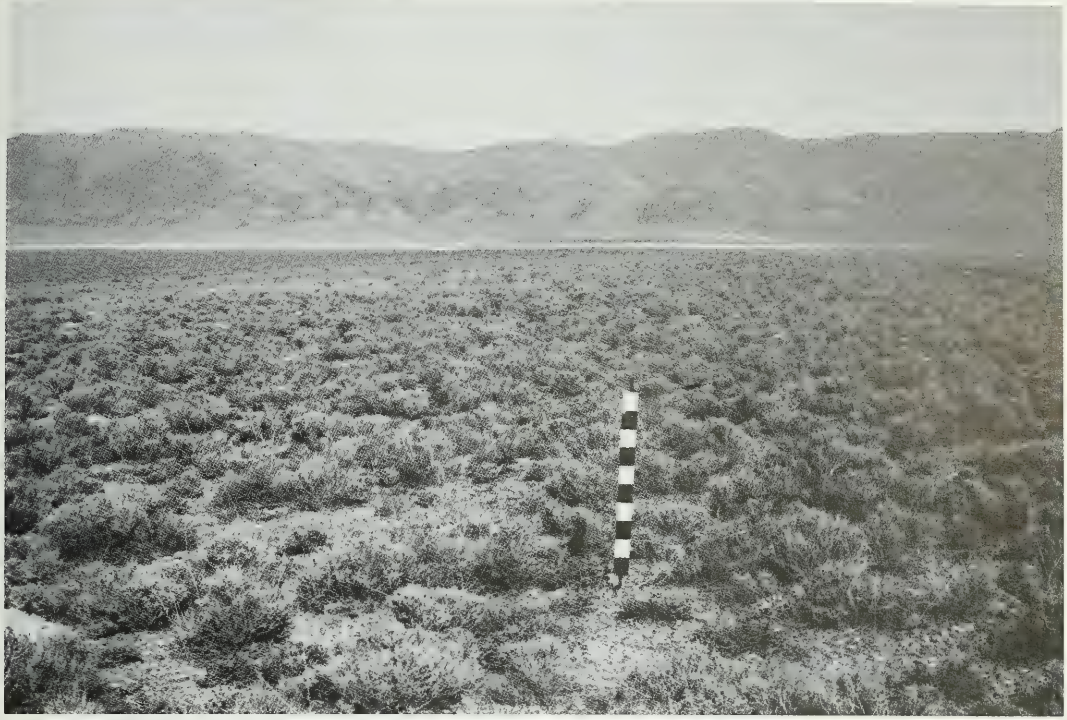

Fig. 12. *Atriplex confertifolia-Artemisia spinescens* located on the north slope of a large gravel bar on the west side of Grass Valley, Nevada.

stands of *S. vermiculatus*, others *A. confertifolia*. Both species are out of place when the surrounding alluvial fans have *A. tridentata* spp. *wyomingensis* plant communities.

The structure of the surface horizon of the lagoon soils, especially in the interspaces between shrubs, greatly limits moisture penetration into the soil profile. In the spring, after winters with below-average precipitation, there is some moisture available for plant growth in soil profiles of *Artemisia* communities. At the same time soils of the lagoons would be completely dry below the surface.

SYNTHESIS OF DYNAMIC LANDFORMS

The basin of pluvial Lake Gilbert is an elongated bowl filled with stairsteplike terraces of predominately clay-sized particles. Atmospheric drought and reduced osmotic potentials caused by soluble salts combine to limit vegetation cover and subsequent protection from erosion.

Water as a mechanism for erosion is restricted in the basin because of lack of precipitation and the porous nature of the surrounding alluvial fans, which largely absorb runoff from the surrounding mountains and limit surface flow. The fine texture of the lake sediments and the limited vegetation cover promote wind erosion. In a previous study in this lake basin, we documented the erosion and subaerial deposition of fine-textured sediments (Young and Evans 1985).

Although we characterized the role of water erosion as restricted, it must not be overlooked or underestimated. Without periodic moisture events that produce stream flow and/or overland flow to eroded rills, gullies, and washes, the development of crypotgamic crust as now exists on the barrier bar would probably stabilize the interspaces among shrubs and protect them against wind erosion. When sufficient water is available on the lake plain to flow, small streams are faced with extremely flat gradients. In addition, the flat gradients are often interrupted by dunes or offshore bars.

Streams tend to meander on the flat lake plains, with loads of sediment being deposited in dune basins and plunge pits. Once the barriers to flow are broken by breaching a barrier bar or dune dam, large amounts of sediment are suddenly available for deposition on the next lower level of the playa itself. Two factors complicate this deposition pattern: (1) the sediments that are moving down the levels in the pluvial basins are loaded with soluble slats, and (2) the redeposited sediment often develops vesicular crust, which limits seedling establishment. These erosion processes, which in a humid climate would have proceeded to a new base level milleniums ago, are retarded to an almost imperceptible pace by the current aridity of the basin.

The erosion and deposition processes are proceeding at a microscale in virtually every location in the basin. On the other end of the scale is the 10 km of braided channels above the dune desert, the erosion of which was instigated when the barrier bar was breached.

The basin of pluvial Lake Gilbert, below the maximum lake level, is composed of dynamic landforms evolved toward a new equilibrium. The landform-soil dynamics provide a fertile template to be colonized and dominated by evolving plant species.

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VEGETATION AND FLORA OF PINE BUTTE FEN, TETON COUNTY, MONTANA

Peter Lesica[1]

ABSTRACT.—The Pine Butte Fen, situated east of the Rocky Mountains in north central Montana, is a boreal, patterned peatland occurring in a relatively dry climatic region. It is one of the southernmost mires of its kind in North America. The vegetation communities present in the fen are described, and possible causes of vegetation patterning are discussed. The Pine Butte Fen is a minerotrophic fen with 93 species of vascular plants represented in an area of approximately 450 ha. Floristic similarities between the Pine Butte Fen and 11 other peatlands in North America reported in the literature are low. Similarity of this fen to other peatlands tends to decrease with increasing distance between the sites and decreasing pH of surface water at other sites. Possible causes for these trends and the floristic uniqueness of the Pine Butte Fen are discussed.

Peatlands (mires) are a common feature in the boreal zones of the earth. Bogs and fens are abundant in northern and central Alberta and Saskatchewan and often cover hundreds of square kilometers in the Hudson Bay Lowlands of Ontario and the Glacial Lake Agassiz region of northern Minnesota (Sjors 1959, Heinselman 1963, Glaser 1983). West of the Continental Divide in Montana, small mires are common in forested areas at low to midelevations where climate is relatively moist and there has been a history of glaciation. East of the Divide mires are generally small and restricted to montane areas. There are no previously published vegetation studies of Montana peatlands.

This study reports the vegetation and flora of the Pine Butte Fen, a large patterned fen in north central Montana situated at the interface of the Northern Great Plains and the east front of the main range of the Rocky Mountains. The Pine Butte Fen is part of the Pine Butte Preserve, a sanctuary established by The Nature Conservancy to protect the last area in the continental United States where large numbers of grizzly bears, *Ursus horribilis*, still migrate onto the plains to feed. Inaccessible and inhospitable terrain has allowed the large wetland complex surrounding Pine Butte to remain the last low-elevation stronghold of the grizzly in the lower 48 states. This report is part of a larger study providing a classification system for and descriptions of the wetland and riparian vegetational communities found in this unique area (Lesica 1982).

Peatlands have been studied extensively in Scandanavia (Sjors 1950, 1980), England (Pearsall and Lind 1941, Pearsall 1955), Canada (Moss 1953, Sjors 1959, Vitt et al. 1975, Slack et al. 1980), and the Great Lakes region of the United States (Heinselman 1963, 1965, 1970, Schwintzer 1978, Schwintzer and Tomberlin 1982, Glaser et al. 1981, Glaser 1983). Good general reviews of the literature concerning peatland vegetation and ecology are provided by Gorham (1957) and Moore and Bellamy (1974). There is a large body of literature dealing with relationships between mire vegetation and water and soil chemistry (Sjors 1950, Jeglum 1971, Waughman 1980, Schwintzer and Tomberlin 1982, Glaser et al. 1981, and Karlin and Bliss 1984). The surface patterning typical of boreal bogs and fens has been discussed by Sjors (1961), Heinselman (1963, 1970), and Glaser (1983).

STUDY AREA

The Pine Butte Fen is on the west side of Pine Butte, approximately 45 km west of Choteau in Teton Co., Montana (47°50′N, 32°30′W, Fig. 1). The fen covers approximately 450 ha on a gentle southeast-trending slope. The Pine Butte area is underlain by glacial outwash derived from calcareous shales and limestones from the main range of the Rocky Mountains that rise abruptly 9 km to the west. Water flowing south from the Teton River through this permeable till rises

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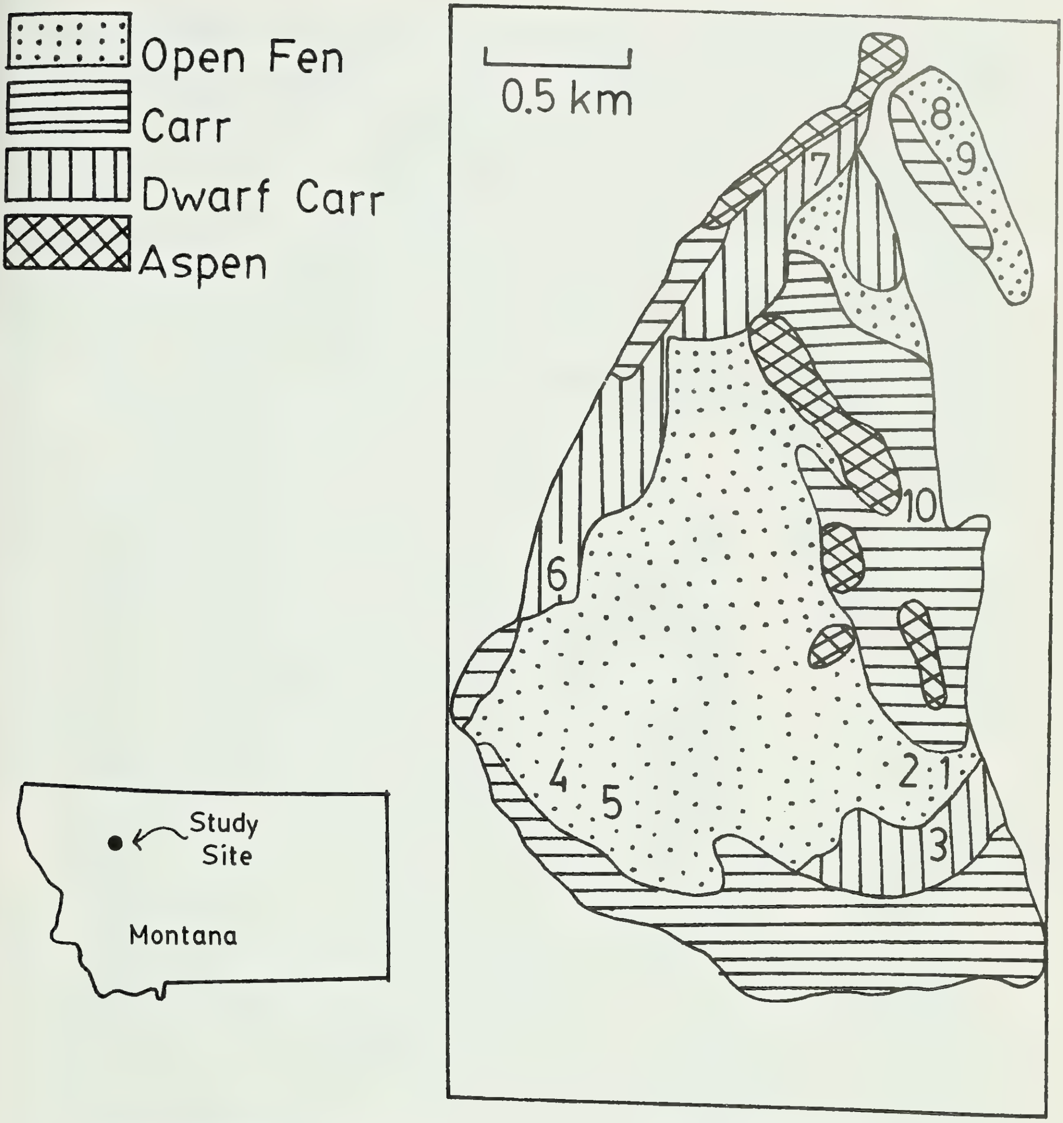

Fig. 1. Vegetation community types in the Pine Butte Fen. Numbers refer to sample stands listed in Table 1.

to the surface in the Pine Butte Fen, providing a nearly constant supply of cold, nutrient-enriched water (Nimick et al. 1983). Fen vegetation occurs on organic soils (peat) 0.5–3.0 m thick. Mean annual precipitation is estimated to be 430 mm and mean annual temperature is 6.0 C (USDA 1980). The precipitation/evaporation ratio along the east front of the Rockies is appreciably lowered by the presence of frequent, strong westerly winds. Upland vegetation surrounding the fen is predominately mixed grass and foothills prairie dominated by grasses such as *Agropyron spicatum*, *Bouteloua gracilis*, and *Stipa comata*. Localized uplifts support open forests dominated by *Pinus flexilis*.

METHODS

I collected plant specimens and made observations during six trips to the study area from May through August 1982. Nomenclature follows Hitchcock and Cronquist (1973) for vascular plants and Crum et al. (1973) for mosses. Specimens were deposited in the herbarium at the University of Montana, Missoula (MONTU).

To characterize the vegetation, I conducted quantitative sampling during the last week in August, essentially following the techniques of Daubenmire (1959). I subjectively placed 10 transects in distinct and homogenous stands of vegetation. For each stand I laid out a 50-m baseline parallel to the slope and placed 20 plots 20 × 50 m at regular intervals along this line. I estimated canopy cover for each species in each plot by assigning it to one of seven classes: T=0–1%, 1=2–5%, 2=6–25%, 3=26–50%, 4=51–75%, 5=76–95%, and 6=96–100%. For each transect, average cover for each species is the mean of the 20 midpoints of the assigned cover classes. I estimated average shrub height to the nearest dm. I determined pH and conductance values of surface water from natural depressions using portable meters. I mapped vegetation using a 1:24000 infrared photograph supplemented by on-site inspection.

Prominence values (PV) were obtained using the formula ($PV=C\sqrt{F}$) where C=% canopy cover and F=absolute frequency (Beals 1960). Sorenson's Index of Similarity (S_s) was computed using the formula $S_s=2w/a+b$ where w=number of the species common to both areas, and a and b are the numbers of species in areas A and B, respectively (Mueller-Dombois and Ellenberg 1974).

RESULTS AND DISCUSSION

Surface Patterning

The Pine Butte Fen displays patterning similar to that of boreal mires and is among the southernmost patterned peatlands in North America, occurring in a region with a relatively low precipitation/evaporation ratio. The recurring pattern found throughout the Pine Butte Fen is one of parallel low ridges (strings) approximately 0.5 m high and 0.5–1.0 m wide alternating with shallow water-filled depressions (flarks) 0.5–2.0 m wide. Strings and flarks lie transverse to the slope, perpendicular to the direction of water movement (Fig. 2). Similar patterned mires have been described by Gorham (1957), Heinselman (1963, 1965), Sjors (1959, 1963), and Glaser et al. (1981).

A number of theories attempt to explain the origin of these patterns. Since strings and flarks are generally found on a slope and are always aligned perpendicularly to it, the most plausible explanation involves gravity. Downhill slippage of peat may result in a series of ridges separated by splits in the surface that fill with water (Pearsall 1955). These rudimentary strings and flarks may then be further differentiated by the relatively higher productivity of the more aerobic string environment. The ponds located at the north end of the Pine Butte Fen, although not extremely elongate, are aligned across slope and may also be the result of downhill slippage (Erman 1976, Moore and Bellamy 1974). Sjors (1961, 1980) feels that string and flark patterns are not caused but merely oriented by the sloping condition. According to his theory, flarks are due to excessive waterlogging, and strings are caused by lateral pressure of ice during freeze-thaw cycles. The regeneration complex theory of Sernander and Von Post and modified by Kulcynski attempts to explain hummock-hollow microtopography in terms of differential growth rates of mosses, principally *Sphagnum* (Moore and Bellamy 1974). A completely satisfactory and all-encompassing explanation for string and flark patterning has yet to be worked out.

Vegetation

Results of the vegetation and water chemistry analysis are presented in Table 1. Based on differences in species composition, development of the shrub layer, and physiognomy of the habitat, the vegetation of the Pine Butte Fen may be divided into three community types (c.t.'s): open fen, dwarf-carr, and carr. The open fen c.t. is further divided into typical and *Scirpus* phases. In some areas of the fen these community types appear distinct; elsewhere they form a continuum.

Water chemistry analyses were too superficial for determining significant correlations; however, pH was consistently lower in the shrub-dominated carr and dwarf-carr c.t.'s. I was unable to detect any correlation between ionic concentration as measured by specific conductance and vegetation. In a study of Swedish mires, Sjors (1950) also found pH to be superior to conductivity as a predictor of vegetation type.

Open fen community type.—Open fen vegetation is dominated by graminoids and

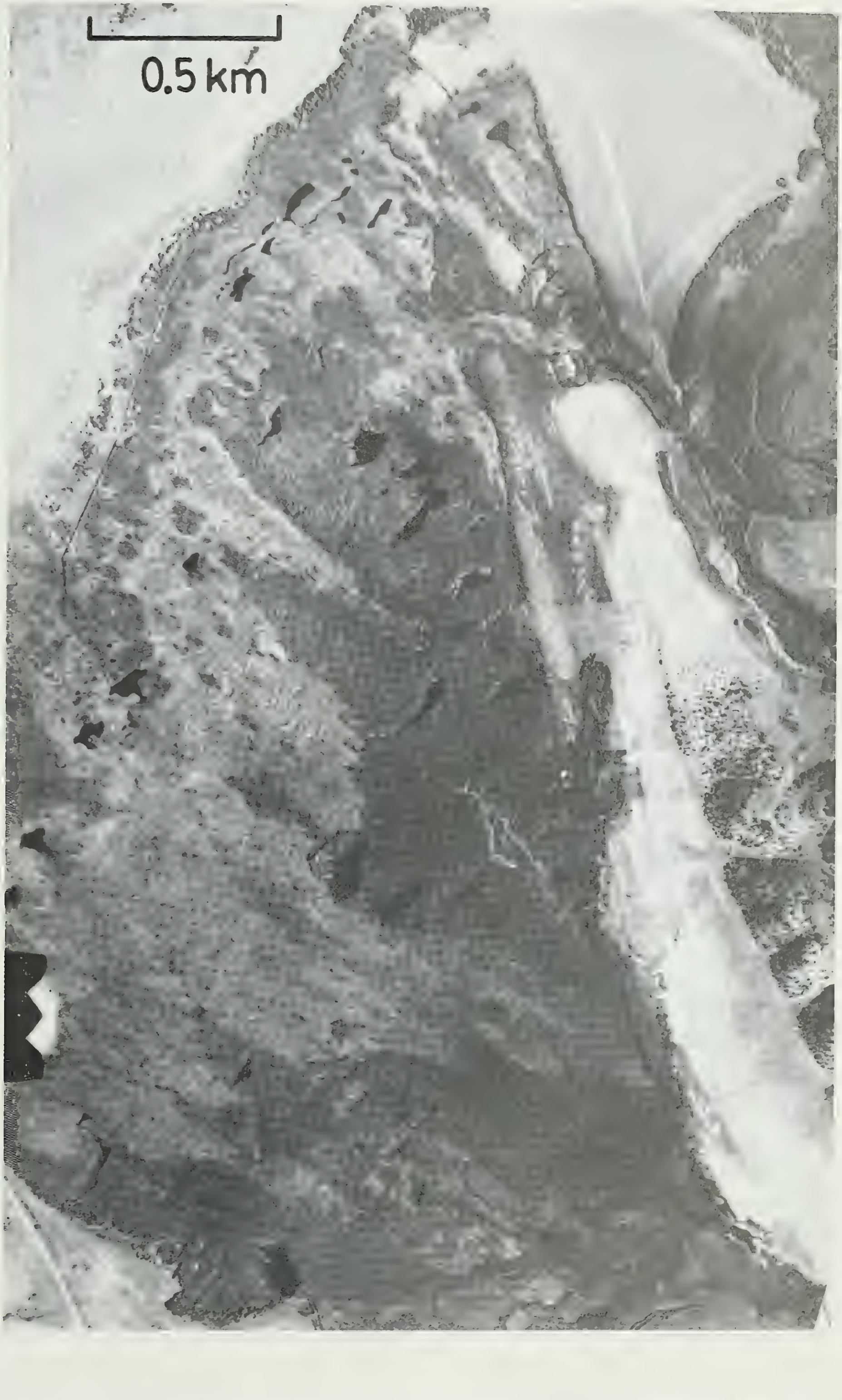

Fig. 2. Aerial photograph of Pine Butte Fen. Note string-flark patterning that appears as parallel wrinkles.

TABLE 1. Species association table for 10 stands in the Pine Butte Fen. Values indicated are prominence values (see Methods). Conductivity and pH measurements were taken from samples of standing water. Stands are grouped by community type.

	Open fen			Open fen Scirpus phase			Dwarf carr			Carr
Stand number	1	4	8	2	5	9	3	7	6	10
Water (%cover)	42	31	45	38	40	54	0	0	5	45
Bare ground	0	0	8	0	0	0	0	0	0	0
Shrub height (dm)	4	4	4	4	4	9	13	18	12	18
Conductivity (umho/cm)	445	520	600	440	490	430	560	395	520	510
pH	7.0	7.1	7.2	7.2	7.1	7.1	6.7	6.8	6.6	6.9
MOSSES										
Drepanocladus revolvens	174	80	17	146	55	0	25	0	3	0
Scorpidium scorpioides	60	25	0	51	29	92	0	0	0	0
Campylium stellatum	178	320	145	206	204	132	158	71	207	1
Rhynchostegiella compacta	0	0	2	0	0	1	29	54	89	1
Calliergon giganteum	0	0	0	0	0	0	0	46	0	0
GRAMINOIDS										
Carex livida	17	9	12	5	6	15	0	0	0	0
Carex limosa	1	52	0	34	113	7	0	0	0	0
Eleocharis pauciflora	2	53	25	68	13	1	3	0	0	0
Muhlenbergia glomerata	25	13	1	3	5	15	0	0	1	0
Carex simulata	250	250	210	38	76	27	0	2	233	0
Scirpus acutus	0	0	0	268	268	256	0	0	0	0
Carex buxbaumii	0	1	0	0	21	0	0	0	1	0
Carex aquatilis	63	1	40	22	0	1	0	165	0	0
Juncus balticus	10	102	46	1	103	37	239	342	197	0
Carex rostrata/aquatilis	—	—	—	—	1	—	170	—	—	311
Carex lasiocarpa	0	0	0	0	0	0	32	17	0	0
FORBS										
Menyanthes trifoliata	279	29	0	136	1	0	0	0	0	0
Utricularia vulgaris	0	0	67	9	11	65	0	0	0	0
Utricularia minor	49	4	1	7	2	11	0	0	0	0
Aster junciformis	7	4	4	18	2	1	2	0	0	0
Galium boreale	42	1	0	64	27	1	23	6	15	0
Triglochin maritima	20	155	151	10	1	7	9	6	23	0
Equisetum laevigatum	0	0	0	0	0	0	1	38	1	47
Equisetum arvense	0	0	0	0	0	0	0	32	0	0
SHRUBS										
Potentilla fruticosa	65	18	21	117	14	20	118	1	22	0
Betula glandulosa	26	26	1	26	33	34	137	41	76	190
Cornus stolonifera	0	0	0	0	0	0	0	18	24	12
Salix candida	2	1	2	2	2	1	1	1	74	2
Salix phylicifolia	0	0	0	0	0	0	1	11	1	75

bryophytes. Shrubs are less than 1.0 m tall with cover values rarely exceeding 30%. This type is associated with poorly drained fibrous peat of the Dougcliff Series (USDA 1980). The surface of the peat displays string and flark patterning, with the flarks containing standing water during all or most of the growing season. In many areas the peat is so unconsoliated and water saturated that the entire surface seems to be floating and "quakes" when stepped on.

The strings are dominated by *Carex simulata, C. aquatilis, Juncus balticus, Muhlenbergia glomeata, Betula glandulosa,* and *Potentilla fruticosa*. Common forbs are *Triglochin maritima, Galium boreale, Aster junciformis, Viola nephrophylla*, and *Dodecatheon pulcherrimum*. The mosses, *Campylium stellatum* and *Drepanocladus revolvens*, form an almost continuous ground layer. Vegetation of the flarks is dominated by the aquatic dicots *Utricularia vulgaris, U. mi-*

nor, and *Menyanthes trifoliata* and the mosses *Scorpidium scorpioides* and *Drepanocladus revolvens*. *Carex simulata*, *C. livida*, and *Eleocharis pauciflora* are common graminoids.

Throughout the open fen are 1–5 ha patches of vegetation dominated by the bulrush *Scirpus acutus*. *Scirpus* is abundant on both strings and flarks, partially replacing *Carex simulata*. *Potentilla fruticosa* and *Betula glandulosa* have greater cover and often attain greater height in these patches than in typical open fen vegetation. All the dominant species of typical open fen vegetation are also associated with the *Scirpus*. Since the small patches of *Scirpus*-dominated vegetation cannot easily be mapped from aerial photographs, this vegetation is best referred to as the *Scirpus* phase of the open fen c.t.

Carr community type.—This community type is dominated by shrubs ranging in height from 1.0 to 3.0 m and attains total cover of greater than 50%. It is associated with mucky peat of the Winginaw Series (USDA 1980). The surface is often of a hummock-hollow microtopography, but distinct strings and flarks do not occur.

Standing water, as much as 0.5 m deep, is often present throughout the growing season. In the Pine Butte Fen, carr vegetation occurs along the margins and occasionally on isolated areas of higher ground.

The hummocks are dominated by *Betula glandulosa*, *Salix monticola*, *S. phylicifolia* var. *planifolia*, *S. serrissima*, and *Cornus stolonifera*. Depressions around the shrubs are dominated by the coarse sedges *Carex rostrata* and *C. aquatilis* and by *Equisetum laevigatum*. Forbs are uncommon, and mosses are present only at the base of shrubs.

Dwarf-carr community type.—Dwarf-carr vegetation is intermediate in appearance and composition to the carr and open fen c.t.'s, and, in some instances, a continuum of all three types occurs. Shrub development is noticeably greater than in the open fen but less than in the carr. Shrubs commonly attain heights of 0.5–2.0 m and cover of greater than 30%. Hummock-hollow microtopography is present, but distinct strings and flarks are generally not apparent. Standing water is present early in the growing season. The dwarf-carr c.t. is most common along the edges of the Pine Butte Fen, but it is also found around ponds and in patches throughout the open fen c.t.

Dominant shrubs are *Betula glandulosa*, *Cornus stolonifera*, *Salix candida*, and *Potentilla fruticosa*. Important herbaceous species are *Carex aquatilis*, *C. simulata*, *C. lasiocarpa*, *Juncus balticus*, *Triglochin maritima*, *Equisetum laevigatum*, *E. arvense*, and *Galium boreale*. Shrubs and most forbs occur only on hummocks, whereas graminoids and *Equisetum* spp. occupy both hummocks and hollows. The mosses *Campylium stellatum* and *Rhyncostegiella compacta* are abundant on hummocks beneath litter.

Narrow bands of vegetation dominated by *Carex rostrata*, *C. sartwellii*, *C. lanuginosa*, and *C. aquatilis* occur occasionally throughout the fen. These bands of coarse sedges run parallel to the slope, and surface water movement is often apparent. Heinselman (1963) refers to similar communities as water tracks. I did not sample this vegetation as it occupies an insignificant portion of the study area.

Aspen (*Populus tremuloides*) dominated vegetation occurs on islands of mineral soil along the east side of the Pine Butte Fen (Fig. 1). These communities were not considered in this study.

Vegetation patterns in the Pine Butte Fen are complex (Fig. 1). Throughout the fen, water percolates up through the underlying mineral substrate (Nimick et al. 1983). Percolation may not be uniform through space. Water appears stagnant in most flarks, but water flow is apparent in small drainages along the margins as well as around ponds and in water tracks. Different rates of water flow may be responsible for much of the vegetation patterning.

Jeglum (1974) states that the two most important environmental gradients affecting the vegetation, floristics, and productivity of peatlands are the moisture-aeration and pH-nutrient regimes (see also Sjors 1950, Gorham 1957, and Heinselman 1970). In saturated organic soils, oxygen is often a limiting factor. Even in mires fed by nutrient-enriched water, phosphorus and nitrogen may be limiting (Slack et al. 1980, Schwintzer and Tomberlin 1982). Areas with increased water flow will have access to greater amounts of oxygen and minerals. It has also been suggested that reducing conditions in peat may promote the accumulation of toxic compounds around subterranean plant organs, a situation that is ameliorated by increased water flow (Moore and Bellamy 1974). Heinselman (1963) found that better tree growth in Minnesota peatlands was correlated with increased water movement, and Ingram (1967) believed that in some cases water movement alone may be responsible for the presence of more eutrophic vegetation.

The open fen community type had the greatest number of species common to bogs and fens throughout boreal North America. Plants such as *Utricularia* spp., *Menyanthes trifoliata, Muhlenbergia glomerata, Carex livida, C. limosa,* and *Eriophorum* spp. are adapted to the poor aeration and nutrient regimes of waterlogged soils (Sjors 1961, Heinselman 1970). Areas occupied by open fen probably have little water movement. The presence of the *Scirpus* phase may indicate somewhat greater water movement, perhaps resulting from increased subsurface upwelling. Lewis and Dowding (1926) and Slack et al. (1980) report similar *Scirpus* communities in Alberta fens occurring along drainage ways, ponds, and other areas of increased water flow.

Carr vegetation is probably associated with soils having relatively better oxygen and nutrient relations. Water movement is often visible in the carr c.t., and beaver activity, generally associated with moving water, is greatest in this vegetation. Greater movement of the water along the margin of the fen is expected in light of the low hydric conductivity of peat (Boelter and Verry 1977). The peat mass acts as a dam, and water, unable to pass over or through it quickly enough, flows around the margin. Moore and Bellamy (1974) attribute the existence of carr vegetation along the margin of a mire in England to the presence of drainage water circumscribing the main peat mass. In a study of peatlands in central Saskatchewan, Jeglum (1971) correlated cover attained by individual species with depth to water table. Water tables ranged from 80 cm below to 60 cm above the soil surface. *Betula glandulosa, Cornus stolonifera*, and five of seven species of *Salix* attained maximum cover values at depth to water table exceeding 20 cm, indicating a preference for the increased aeration of the better drained soils. In the Pine Butte Fen, *Betula, Cornus*, and *Salix* attained maximum height and cover values in the carr c.t., probably responding to the more favorable conditions provided by greater water movement or better aerated soil. The dwarf-carr c.t., intermediate in shrub development, is probably also intermediate in its requirements for nutrients and oxygen in the rooting zone.

An alternative explanation for the distribution of vegetation in the Pine Butte Fen follows the lines of classic hydrarch succession in which the direction of change is from an aquatic to a terrestrial environment (Oosting 1948). Aquatic plants are replaced by herbaceous emergents, which are in turn replaced by woody plants that increase transpiration and lower the water table (Dansereau and Segadas Vianna 1952). Since the peripheral carr vegetation frequently has deeper surface water than the center of the mire, a simple explanation based on hydrarch succession seems untenable. Although the major vegetation patterns displayed in the Pine Butte Fen can be accounted for by a theory based on the movement of water, confirmation of this theory requires thorough analysis of water chemistry throughout the fen.

Floristics

I observed 93 species of vascular plants and nine species of mosses in the Pine Butte Fen (Appendix A). I believe the vascular plant list to be nearly complete, whereas the list of bryophytes is certainly incomplete and probably includes only the most common moss species. The majority of vascular species occurred on hummocks, often in association with shrubs. Many, such as *Fragaria virginiana, Galium boreale, Senecio pauperculus, Smilacina stellata,* and *Vicia americana,* although common in the fen, were at least as common in adjacent upland communities. A much smaller number of species was found in the standing water of depressions. Moore and Bellamy (1974) state that low oxygen tensions associated with waterlogged soils is one of the major problems faced by peatland vegetation. Possibly the better aeration of the hummock soils provides a habitat suitable to many species not specifically adapted to mires. Eleven species of vascular plants found in the Pine

TABLE 2. Floristic similarities between the Pine Butte Fen and other peatlands in North America. S_s = Sorenson's Index of Similarity (see Methods for explanation). Ericads = number of woody ericaceous species present.

Location and reference	S_s	Distance (km)	pH	Ericads
Slack et al. (1980) Alberta. Rich fens.	28	650	6.8–7.9	4
Jeglum (1971) Saskatchewan. Eutrophic peatlands.	27	850	6.0–7.9	4
Vitt et al. (1975) Alberta. Poor fens.	8	900	5.0	8
Baker (1972) California. Fen.	7	1350	5.2–7.0	1
Heinselman (1963) Minnesota. Patterned fens.	18	1400	5.3–6.4	3
Glaser et al. (1981) Minnesota. Rich fens.	17	1400	4.3–6.9	6
Sjors (1963) Ontario. Rich fens.	24	2000	5.8–7.1	5
Schwintzer (1978) Michigan. Fens.	10	2250	5.7–7.0	3
Vitt and Slack (1975) Michigan. Bogs and fens excluding forest.	9	2200	4.9–6.7	11
Montgomery and Fairbrothers (1963) New Jersey. Bogs.	1	3150	—	10
Drury (1956) Alaska. Bogs.	19	4000	—	8

Butte Fen are restricted to bogs and fens throughout their range (Appendix A). A major environmental factor influencing mire vegetation is the mineral concentration and coincident hydrogen ion concentration (pH) of the water (Waughman 1980). A gradient of ombrotrophic (mineral-poor, low pH) to minerotrophic (mineral-enriched, high pH) water determines the continuum of bog to rich fen (Sjors 1950). Ombrotrophic bogs are characterized by "acid-loving" species-poor floras, whereas minerotrophic rich fens typically have a greater number of vascular species, some of which are calciphiles (Gorham 1957). Karlin and Bliss (1984) feel that the greater species diversity of strongly minerotrophic mires is a reflection of the complex interactions of microrelief and substrate chemistry gradients. The Duhr Fen displays a high species diversity common to rich fens, and many of the common mosses, such as *Scorpidium scorpioides*, *Drepanocladus revolvens*, and *Campylium stellatum*, are considered rich fen indicators (Sjors 1950, Slack et al. 1980).

Many bogs and fens throughout North America have been studied floristically. Although vascular plant species lists reported for other mire systems may be incomplete, comparisons using Sorenson's Index of Similarity (S_s) indicate degree of relationship and point to factors controlling floristic differences (Table 2). In general, floristic similarity to the Pine Butte Fen decreases with decreasing pH and increasing distance of separation. All other mire systems reported in the literature that I surveyed have at least one species of ericaceous shrub, and, in those cases where bryophytes were also included, all have at least one species of *Sphagnum*. Rich fens in Alberta and Saskatchewan show the greatest similarity to the Pine Butte Fen; however, none of the bogs and fens surveyed have a similarity to the Pine Butte Fen greater than 30%. In contrast, Wheeler et al. (1982) found much greater similarity between their study area in northern Minnesota and peatlands in Ontario, Saskatchewan, and Michigan ($S_s >$ 40%).

A major factor responsible for the floristic uniqueness of the Pine Butte Fen is climate. Bogs and fens generally occur in regions with a cool, moist climate (Dansereau and Segadas-

Vianna 1952, Sjors 1961). Walther and Leith (1960) have prepared world climatic zone maps based, in part, on length of growing season and precipitation/evaporation ratios. These maps place the Pine Butte Fen in the arid continental zone, whereas all other patterned fens of significant size reported in the literature for North America occur in more mesic zones (e.g., typical temperate, warm temperate, boreal, and arctic). The aridity of the Pine Butte area may account for the distinctness of its peatland flora in two ways. First, *Sphagnum* spp. are important components of most northern mire vegetation, and, although *Sphagnum* can establish in calcareous regions (Gorham 1957, Heinselman 1963), it grows only in moist areas (Moss 1953). The absence of *Sphagnum* and the localized acidity associated with it may be responsible for the absence of ericaceous shrubs, *Drosera* spp., and other "acid-loving" species from the Pine Butte Fen. Secondly, a large number of species found in the Pine Butte Fen are derived from adjacent upland communities and are adapted to the regional aridity. Many of these species are not available to mire systems occurring in different climatic regions. The presence of nutrient-enriched groundwater, the microtopographic heterogeneity due to the various surface patterns, the large size of the mire, and the relatively xeric climate of the region are undoubtedly all factors contributing to the large and unique flora of the Pine Butte Fen.

ACKNOWLEDGMENTS

I am grateful to Gerald Moore and David McAllister for assistance in the field. Robert Dorn identified the willows, and Bruce McCune determined a number of the mosses. Anne Bradley and Robert Antibus gave helpful criticisms on the manuscript. Joanne Antibus provided the illustrations, and Susan Molina typed the manuscript. Funding was provided by The Nature Conservancy.

APPENDIX A

List of vascular plants and bryophytes of the Pine Butte Fen. The * indicates species that are restricted to bogs and fens throughout their range.

APIACEAE
Cicuta douglasii (DC.) Coult. & Rose

ASTERACEAE
Antennaria pulcherrima (Hook.) Greene
Antennaria microphylla Rydb.
Aster junciformis Rydb.
Aster occidentalis (Nutt.) Torr. & Gray
Crepis runcinata (James) Torr. & Gray ssp. *hispidulosa* (Howell) Babc. & Stebb.
Helianthus nuttallii Torr. & Gray
Senecio pauperculus Michx.
Solidago canadensis L. var. *salebrosa* (Piper) Jones
Solidago nemoralis Ait. var. *longipetiolata* (Mack. & Bush) Palmer & Steyerm.
Taraxacum laevigatum (Willd.) DC.
Taraxacum officinale Weber

BETULACEAE
**Betula glandulosa* Michx. var. *glandulosa*

CAMPANULACEAE
Campanula rotundifolia L.
Lobelia kalmii L.

CORNACEAE
Cornus stolonifera Michx. var. *stolonifera*

CYPERACEAE
Carex atherodes Spreng.
Carex aquatilis Wahl.
Carex aurea Nutt.
Carex buxbaumii Wahl.
Carex capillaris L.
Carex diandra Schrank
Carex dioica L. var. *gynocrates* (Wormsk.) Ostenf.
Carex disperma Dewey
Carex interior Bailey
Carex lanuginosa Michx.
Carex lasiocarpa Ehrh. var. *americana* Fern.
**Carex limosa* L.
**Carex livida* (Wahl.) Willd.
Carex nebrascensis Dewey
Carex oederi Retz. var. *viridula* (Michx.) Kuek.
Carex rostrata Stokes
Carex sartwellii Dewey
Carex scirpoidea Michx. var. *scirpoidea*
Carex simulata Mack.
Eleocharis palustris (L.) R. & S.
Eleocharis pauciflora (Lightf.) Link
**Eriophorum polystachion* L.
**Eriophorum viridicarinatum* (Engelm.) Fern.
Scirpus acutus Muhl.

EQUISETACEAE
Equisetum laevigatum A.Br.
Equisetum variegatum Schleich.

ERICACEAE
Pyrola asarifolia Michx. var. *asarifolia*

FABACEAE
Vicia americana Muhl. var. *truncata* (Nutt.) Brew.

GENTIANACEAE
Gentiana amarella L.
Gentiana dentosa Rottb.

IRIDACEAE
Iris missouriensis Nutt.

JUNCACEAE
Juncus alpinus Vill.
Juncus balticus Willd. var. *montanus* Engelm.

JUNCAGINACEAE
Triglochin maritimum L.
Triglochin palustre L.

LENTIBULARIACEAE
**Utricularia minor* L.
Utricularia vulgaris L.

LILIACEAE
Allium schoenoprasum L.
Lilium philadelphicum L.
Smilacina stellata (L.) Desf.

MENYANTHACEAE
**Menyanthes trifoliata* L.

ONAGRACEAE
Epilobium palustre L.

ORCHIDACEAE
Corallorhiza trifida Chat.
Cypripedium calceolus L. var. *parviflorum* (Salisb.) Fern.
Habenaria hyperborea (L.) R.Br.
Spiranthes romanzoffiana Cham. var. *romanzoffiana*

POACEAE
Agropyron caninum (L.) Beauv. var. *unilaterale* (Vasey) Hitchc.
Agrostis alba L. var. *alba*
Bromus ciliatus L.
Calamagrostis inexpansa Gray var. *inexpansa*
Deschampsia cespitosa (L.) Beauv. var. *cespitosa*
**Muhlenbergia glomerata* (Willd.) Trin.
Muhlenbergia richardsonis (Trin.) Rydb.

POLEMONIACEAE
Phlox kelseyi Britt. var. *kelseyi*

PRIMULACEAE
Dodecatheon pulchellum (Raf.) Merrill var. *pulchellum*
Lysimachia thrysiflora L.

RANUNCULACEAE
Anemone parviflora Michx.
Thalictrum venulosum Trel.

ROSACEAE
Fragaria virginiana Duchesne var. *glauca* Wats.
Potentilla fruticosa L.
Potentilla gracilis Dougl. var. *elmeri* (Rydb.) Jeps.

RUBIACEAE
Galium boreale L.

SALICACEAE
Salix bebbiana Sarg. var. *perrostrata* (Rydb.) Schneid.
**Salix candida* Fluegge
Salix drummondiana Barratt
Salix monticola Bebb.
Salix myrtifolia Anderss.
Salix phylicifolia L. var. *planifolia* (Pursh) Hiit.
Salix rigida Muhl. var. *watsonii* (Bebb.) Cronq.
**Salix serrissima* (Bailey) Fern.

SAXIFRAGACEAE
Parnassia palustris L.
Scrophulariaceae
Castilleja miniata Dougl. var. *miniata*
Castilleja sulphurea Rydb.
Pedicularis groenlandica Retz.

VALERIANACEAE
Valeriana edulis Nutt. var. *edulis*

VIOLACEAE
Viola adunca Sm. var. *adunca*
Viola nephrophylla Greene var. *cognata* (Greene) Hitchc.

MOSSES
Bryum pallescens Schleich.
Calliergon giganteum (Schimp.) Kindb.
Campylium stellatum (Hedw.) C.Jens.
Drepanocladus exannulatus (S.S.G.) Warnst.
Drepanocladus revolvens (Sw.) Warnst.
Mnium rugicum Laur.
Platydictya jungermanioides (Brid.) Crum
Rychostegiella compacta (C. Muell.) Loeske
Scorpidium scorpioides (Hedw.) Limpr.

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EFFECTS OF SUSPENDED SEDIMENT ON LEAF PROCESSING BY *HESPEROPHYLAX OCCIDENTALIS* (TRICHOPTERA: LIMNEPHILIDAE) AND *PTERONARCYS CALIFORNICA* (PLECOPTERA: PTERONARCIDAE)[1]

C. Evan Hornig[2] and Merlyn A. Brusven[2]

ABSTRACT.—The effects of suspended sediments on stream invertebrate detrital processing were investigated under replicated conditions in light and temperature-controlled chambers in the laboratory. The leaf-shredding insects *Pteronarcys californica* and *Hesperophylax occidentalis* were studied. Mean daily ingestion rates were lower among insects subjected to suspended sediments (1.5 and 3.0 g/l) than insects held in suspended sediment-free environments for seven of the eight trials. In five of the eight trials, mean ingestion rates were suppressed by ≥41% when compared to insects held in suspended sediment-free environments. Feeding inhibition was typically greater at the end of the feeding trials (14 days) than at the beginning (0-4 days). The effects of suspended sediments on ingestion were apparently related to the feeding status of the insects at the time of a trial. Insects in an active feeding mode were less influenced by suspended sediment than those in an inactive feeding mode. We conclude that, depending on the season and the duration of impact, suspended sediment can suppress processing of coarse particulate organic matter and thus adversely influence important nutrient and energy pathways in low-order streams.

Inorganic sediment introduction is a common and ubiquitous cause of water quality deterioration. Certain practices used in agriculture, forestry, road construction, mining, and urban development may contribute to increased sediment loads of streams. The effects of bottom sedimentation on macroinvertebrate distribution and community structure have been well documented (Brusven and Prather 1974, Cordone and Kelley 1961, Cummins and Lauff 1969, Lemly 1982). Bjornn et al. (1977) found that different quantities of sediment and the degree to which cobbles were imbedded by fine sediments differentially affected species within the macroinvertebrate community.

Sedimentation can also affect the size of insect populations through degradation of food resources. Reice (1980) reported that leaf litter decomposition was less in silt than on coarse-particle sediments; Herbst (1980) reported decreased insect consumption of previously buried leaves.

The effects of suspended sediments on stream insects are poorly understood. Field investigations have shown that high suspended sediment loads cause increased insect drift (Rosenberg and Wiens 1975, White and Gammon 1977, O'Hop and Wallace 1983). Although most suspended sediments are apparently not acutely toxic to aquatic life (Brusven and Hornig 1984, Oxberry et al. 1979), stressful responses, such as catastrophic drift, have been documented and prompted us to study other sublethal effects. Our study was designed to investigate the effects of suspended inorganic sediment on the degradation of leaf litter by stream insects.

MATERIALS AND METHODS

Suspended sediment experiments were conducted in 10 1-liter glass beakers filled with 0.9 liter of unchlorinated tap water. These vessels were placed in a temperature bath held at 5 C ± 1 to minimize algal growth. A magnetic stirrer was positioned in the bottom of each vessel to maintain water circulation and oxygen saturation. A 1.2-mm mesh screen was placed 3 cm above the magnetic stirrer in each beaker to protect the insects from injury. Photoperiod was controlled by timers attached to four 1.2-m fluorescent-light tubes suspended 0.6 m above the vessels. For all but one experiment (trial), the dark-light conditions were set at 12-12 h. A 6-18 h dark-light cycle was used to induce feeding by the experimental animals in December.

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[1] Research supported in part by the United States Department of the Interior, Office of Water Research and Technology Agreement 371402. Approved by the director of the Idaho Agricultural Experiment Station as Research Paper 8578.

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TABLE 1. Mean daily ingestion rates for *Hesperophylax occidentalis* larvae exposed to two levels of suspended sediment (1.5 and 3.0 g/l) and those for control larvae. (Trial duration: 14 days; individuals per treatment: 5; t and p values calculated using Student's paired t test.)

Age class	Sediment concentration level	Mean daily ingestion rate (mg/day)			
		Control insects	Test insects	t	p
Early instar	1.5 g/l	0.42	0.21	2.06	0.11
Early instar	3.0 g/l	1.22	1.19	0.17	0.87
Late instar	1.5 g/l	1.47	0.86	1.38	0.24
Late instar	3.0 g/l	1.81	0.85	2.10	0.10

TABLE 2. Mean daily ingestion rates for *Pteronarcys californica* naiads exposed to two levels of suspended sediment (1.5 and 3.0 g/l) and those for control naiads (Trial duration: 14 days; individuals per treatment: 5; t and p values calculated using Student's paired t test).

Age class	Sediment concentration level	Mean daily ingestion rate (mg/day)			
		Control insects	Test insects	t	p
First-year	1.5 g/l	1.29	1.13	0.93	0.40
First-year	3.0 g/l	0.57	0.24	2.43	0.07
Second-year	1.5 g/l	1.70	0.76	2.09	0.10
Second-year	3.0 g/l	9.49	9.97	0.93	0.40

The stream insects tested were the caddisfly *Hesperophylax occidentalis* (Banks) and the stonefly *Pteronarcys californica* Newport. These insects are primarily leaf-shredders (Merritt and Cummins 1978). *Hesperophylax occidentalis* is found in small mountain streams of the western United States (Martinson and Ward 1982), whereas *P. californica* is common in larger streams of the region (Elder and Gaufin 1964). Early- and late-instar larvae of *H. occidentalis* and first- and second-year naiads of *P. californica* were used to assess age-specific responses to suspended sediments. Insects were collected in the field and acclimated to laboratory conditions for a minimum of four days prior to testing. All organisms were starved for two days prior to testing.

Alder (*Alnus rubra*) leaves were used as the food in all trials. The leaves were conditioned for one month in unchlorinated tap water held at 4 C; in winter feeding trials the leaves were held for two to four months. The suspended sediment material was commercially graded white sand sieved through a 75-μm mesh screen and added to the test chambers as a slurry. Sediments were maintained in suspension by water circulation from the magnetic stirrers.

Two suspended sediment concentrations (1.5 g/l and 3.0 g/l) were tested against a control concentration of 0.0 g/l on each of the two nymphal or larval age classes and two insect species for a total of eight trials. For each trial, 12 vessels were arranged in pairs in a continuously circulating, temperature-controlled bath. Five pairs of vessels were used to determine insect feeding rates in suspended sediment and sediment-free environments; the sixth pair of vessels was used to hold and condition leaf disks in suspended and nonsuspended sediment conditions similar to the other five pairs, but in the absence of insects. Disks placed in the sixth pair of vessels were used as "blanks" and provided a correction factor caused by leaf leaching or decomposition during a trial. One vessel (test vessel) from each pair was randomly selected for sediment introduction, but the other vessel (control vessel) remained free of sediment. This design avoided the segregation of test and control replicates that may occur with a completely randomized design (Hurlbert 1984). Each trial was conducted for 14 days, with one insect placed in each of the 10 experimental vessels for the duration of a trial.

Five leaves were used to initially supply leaf disks to the five pairs of test and control vessels, with one leaf per vessel pair distributed as follows. Two pairs of leaf disks (each disk 18 mm in diameter) were cut from the leaf with a cork borer. One disk from the first pair was placed in the test vessel and the pair's other disk in an insect-free container. The second pair of disks was similarly distributed to the matching control vessel and an insect-free container. Leaf consumption was estimated as the difference in ash-free dry weight (AFDW) between the disk of each pair placed in the insect-free container and the corresponding disk placed in a test or control vessel. This procedure allowed direct measurement of leaf loss due to insect feeding and is similar to that described by Grafius and Anderson (1979). Depending on leaf utilization, the residual coarse leaf material was replaced with new leaf disks at two- to seven-day intervals.

Results

Mean daily ingestion rates were less among test than control insects for seven of the eight trials, but were not significantly different at $p=0.05$ (Tables 1 and 2). In five of the eight trials, mean ingestion rates were substantially suppressed (41% to 58%) when compared to the corresponding controls. When averaged over the trial duration, the mean ingestion rate appeared to be unrelated to species, age class, or the two suspended sediment concentrations tested (1.5 and 3.0 g/l). However, the length of time insects were exposed to suspended sediment apparently influenced their feeding rates.

Feeding inhibition among test insects was more evident at the end rather than the beginning of each trial (Figs. 1-4). The debilitating effect of prolonged exposure to suspended sediment was particularly pronounced among the early-instar *H. occidentalis* larvae exposed to 3 g/l suspended sediment. Whereas the mean ingestion rate of test and control insects was similar during the first 12 days of exposure to suspended sediment, the leaf consumption rate of test insects was only 12% of the control insect consumption rate during the final 2 days of the trial.

Discussion

Our results indicate that inert suspended solids, although not acutely toxic at high levels, may cause sublethal effects on aquatic invertebrates by reducing feeding activity. Impacts on the biological functioning of large-particle detritivores (shredders) such as the species tested in this study may have serious ramifications on other biotic components of the ecosystem. In small, first-to-third order streams riparian vegetation often shades the stream, suppresses algal growth, and supplies the stream with coarse particulate organic matter. These ecosystems are highly dependent on allocthonous material as a primary source of energy (Anderson and Sedell 1979). Processing of large-particle detritus by shredder invertebrates provides fine-particle detritivores energy and nutrients from fecal production. For example, Short and Maslin (1977) found that in laboratory streams supplied with alder leaves, *Pteronarcys californica* increased the food availability to *Hydropsyche* by 35%–100% and to *Simulium* by 600%–700%. Grafius and Anderson (1979) found that although the production of the leaf shredder *Lepidostoma quercina* was itself a minor component in a small Oregon stream, the feces produced by this insect supported 20%–50% of the more abundant simuliid population found in the creek. This is not surprising, because the fecal production rate of *Lepidostoma* has been calculated to be 50 times its growth rate (Grafius and Anderson 1980).

We believe the differences we observed in the feeding rates of our control insects may be related to a physio-ecological response keyed to the season when the specimens were collected in the field. We were unable to induce noticeable feeding activity in the December-collected, first-year *P. californica* naiads until the dark-light cycle was altered to 6-18 h. Feeding rates for these insects were still much lower than first-year *P. californica* naiads collected in November. Among the second-year *P. californica* naiads tested, those collected in October had higher feeding rates than those collected during August. Water temperature and food availability should theoretically make autumn the most opportune time for feeding by leaf-shredding insects.

The early-instar *H. occidentalis* larvae collected in mid-February had higher ingestion rates than those collected during early January. Field observations at the collection site suggest that greatest larval growth occurs during early spring. Rapid growth is likely induced by seasonal cues such as photoperiod

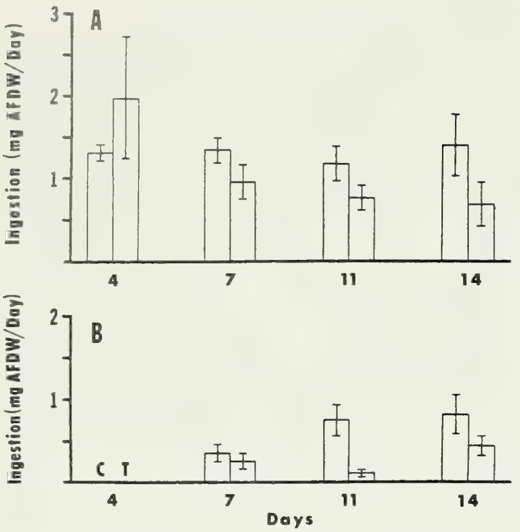

Fig. 1. Mean daily ingestion rates (mg AFDW/day) for first-year naiads of *Pteronarcys californica* exposed to: A, 1.5 g/l. B, 3.0 g/l suspended sediment for 14 days. C = control insects, 0.0 g/l suspended sediment; T = test insects. Vertical lines = 95% confidence interval for mean ingestion rate.

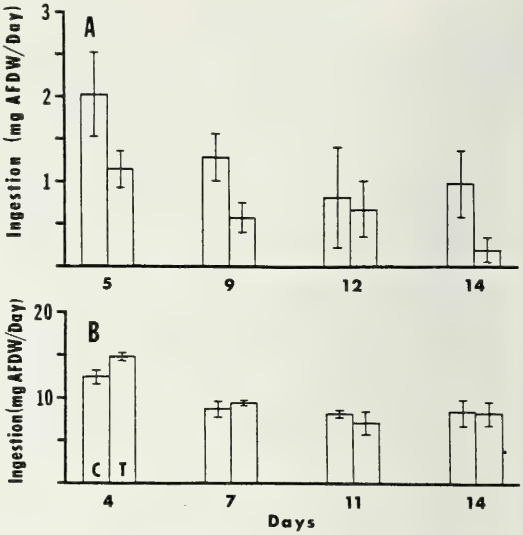

Fig. 2. Mean daily ingestion rates (mg AFDW/day) for second-year naiads of *Pteronarcys californica* exposed to: A, 1.5 g/l. B, 3.0 g/l suspended sediment for 14 days. C = control insects, 0.0 g/l suspended sediment; T = test insects. Vertical lines = 95% confidence interval for mean

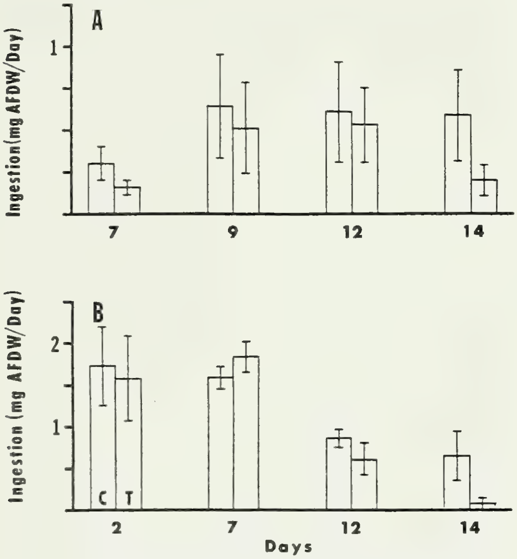

Fig. 3. Mean daily ingestion rates (mg AFDW/day) for early-instar larvae of *Hesperophylax occidentalis* exposed to: A, 1.5 g/l. B, 3.0 g/l suspended sediment for 14 days. C = control insects, 0.0 g/l suspended sediment; T = test insects. Vertical lines = 95% confidence interval for mean ingestion rate.

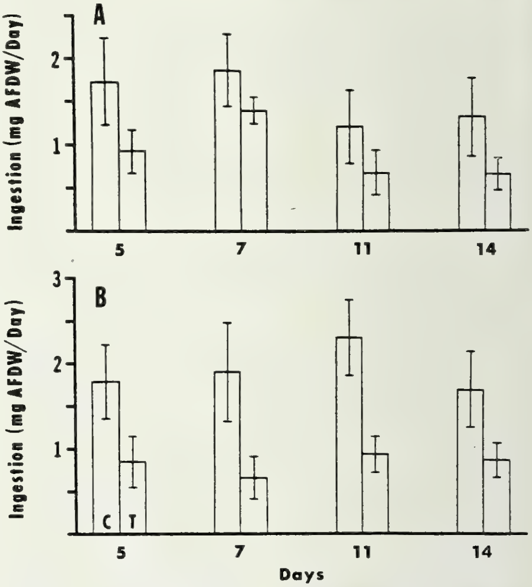

Fig. 4. Mean daily ingestion rates (mg AFDW/day) for late-instar larvae of *Hesperophylax occidentalis* exposed to: A, 1.5 g/l. B, 3.0 g/l suspended sediment for 14 days. C = control insects, 0.0 g/l suspended sediment; T = test insects. Vertical lines = 95% confidence interval for mean ingestion rate.

and temperature. Similar growth responses have been reported for other insects by Beck (1980), Hynes (1970), and Lutz (1974).

Another factor that may have affected feeding rates between trials was the conditioning time of the leaf material (Golladay et al. 1983). In our study, leaf disks used during our winter trials were conditioned for longer than one month; however, there was little evidence to support differential feeding rates between leaves conditioned for one month vs. those conditioned for 2-4 months.

The effect of suspended sediment on invertebrate ingestion appears to be largely influenced by the season and feeding status of the insects. Feeding rates of insects in a relatively active feeding mode, as reflected by the control specimens, may not be as affected by suspended sediment as insects in a less active feeding mode. We speculate that the short-term effects of suspended sediments on feeding rates of insects vary seasonally. Our study provides evidence that prolonged exposure to suspended sediments can adversely affect both actively and nonactively feeding insects by reducing their mean daily ingestion rates.

Previous research on the sublethal effects of suspended sediments on leaf processing by aquatic invertebrates is minimal and largely limited to zooplankton studies (Arruda et al. 1983, McCabe and O'Brien 1983). These studies demonstrated that suspended sediments can decrease feeding rates of *Daphnia* spp. by at least 90%. These filter-feeders ingested large quantities of silt from the water column, which resulted in dense packing of the gut with inorganic particles. A decreased filtering rate is likely caused by excessive gut loading (McCabe and O'Brien 1983). Although the sediment ingestion rate would likely be lower among nonfilterers, it may have been a factor influencing the early-instar *H. occidentalis* larvae, which diplayed a sudden decrease in feeding after 12 days' exposure to 3 g/l suspended sediment in our study.

Nontoxic materials, such as inorganic silt, or sublethal concentrations of toxicants may not cause spectacular and immediate impacts on aquatic macroinvertebrates, but they may cause a reduction in secondary production, energy-transfer efficiency, and nutrient cycling in stream ecosystems.

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EFFECTS OF WATERSHED ALTERATION ON THE BROOK TROUT POPULATION OF A SMALL BLACK HILLS STREAM

Timothy Modde[1], Henry G. Drewes[1], and Mark A. Rumble[2]

ABSTRACT.—The impacts of adjacent landscaping activity and livestock presence on the brook trout (*Salvelinus fontinalis*) population of a small Black Hills stream were evaluated. Moderate changes in temperature, turbidity, and fecal coliform numbers did not influence brook trout densities. Stream morphometry, particularly factors affecting stream cover, appeared to have the greatest impact on numbers of trout. Brook trout were poor indicators of moderate changes in water quality, but they were adequate indicators of the physical perturbations within the stream.

The aquatic biota of streams within the forests of our nation are being increasingly stressed by logging, livestock grazing, mining, road construction, and residential development. Impacts of these activities on streams are often manifested by changes in water quality or through physical changes in the habitat, such as channel modification or reduction in stream flow. Such environmental changes can produce biological responses that alter composition and abundance of resident species. Organisms sensitive to environmental change function as indicators of environmental modification and may be useful in evaluating the magnitude of an impact.

Not all aquatic organisms exhibit equal sensitivity to the same stresses, however. Aquatic invertebrates are sensitive to water quality changes resulting from organic enrichment (Hilsenhoff 1977, Jones et al. 1981) and toxic pollutants (Hocutt 1975) but are not always effective in evaluating moderate physical modifications (Marsh and Waters 1980). Conversely, because of their mobility, Price (1979) suggested that fishes may not be reliable indicators of change in water quality, although fish frequencies do respond to changes in structure of the habitat (Platts 1974, Binns and Eiserman 1979).

The objective of this study was to evaluate the response of a resident brook trout (*Salvelinus fontinalis*) population to water quality and habitat changes in a small Black Hills stream subjected to landscaping activities (clearcutting an adjacent slope and pond dredging) and intermittent livestock grazing within the watershed.

METHODS

The study area included five sampling stations within the upper Slate Creek watershed (Fig. 1) in Pennington County, South Dakota. Two stations were established above a development site within the watershed, one on South Slate Creek and the other on Slate Creek proper, both first order streams. A third sampling station was located 0.1 km downstream from the development site on Slate Creek; two additional stations were established downstream at approximately 1.0 km intervals. Stations above the construction site were not exposed to grazing except for a confined watering site above station 1, whereas stations below the construction site were exposed to grazing during the late fall and winter months.

Twelve water quality variables were measured at three-week intervals during the spring and summer of 1981 and 1982. During the period between August 1981 and April 1982, water samples were collected at intervals ranging between six and eight weeks. Total hardness, alkalinity, dissolved oxygen, pH, and conductivity were determined onsite with field analysis units. Turbidity, total phosphorus (ortho and total), nitrogen (Kjeldahl and ammonia), and fecal coliform bacteria were determined in the laboratory.

Fishes were collected from each station by electrofishing a 61 m section of stream blocked from both directions by 6.4 mm mesh seines. Population estimates were repre-

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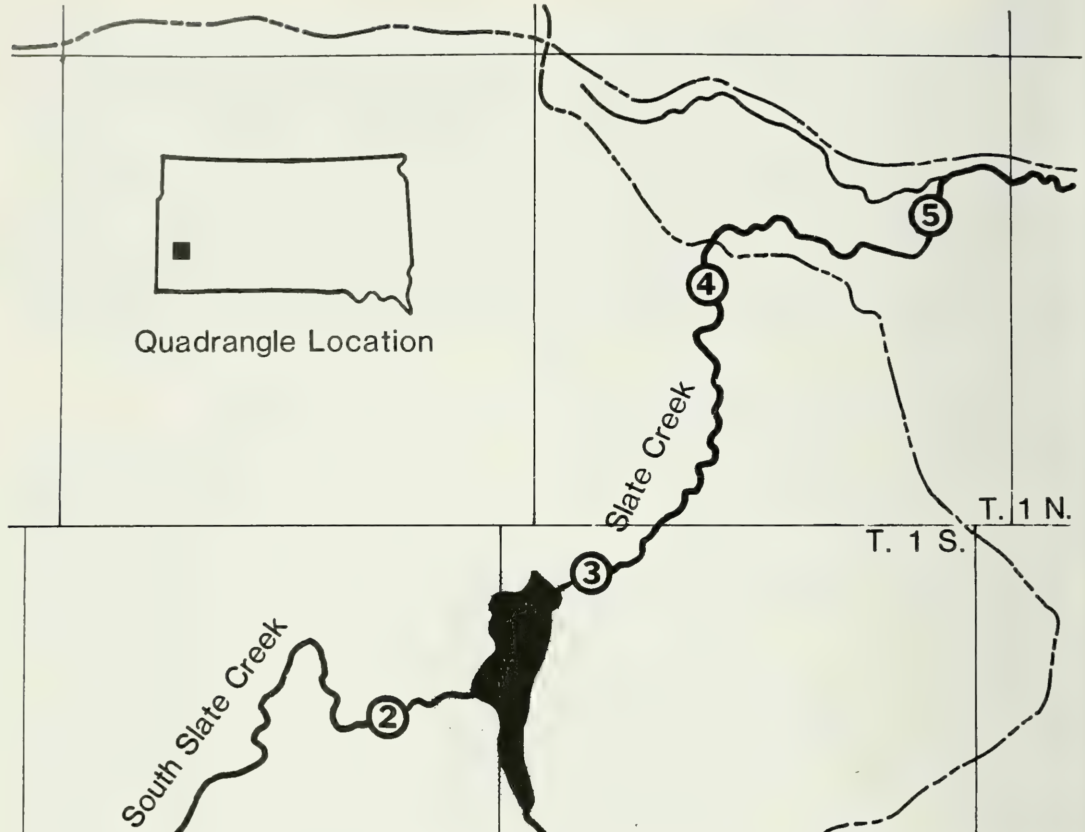
Quadrangle Location
Slate Creek
South Slate Creek
Slate Creek
T. 1 N.
T. 1 S.
R. 3 E.
R. 4 E.
N
0
0.5
1.0km
1
2
3
4
5
LEGEND
Excavated Lake Basin
Construction Site
Stream Channel
Hard Surface Road
Sampling Station

Fig. 1. Map indicating location of the five sampling stations in relation to the Deerfield Park development site in Pennington County, South Dakota.

sented by the total number of fish collected in two consecutive electroshocking passes. Length and weight of brook trout were recorded and scale samples taken during each collection. Fish were sampled at approximately six-week intervals between 9 June 1981 and 29 August 1981 and between 24 May 1982 and 12 August 1982. Because of the absence of flow from the electroshocking site at station 2 during 1981, no fish were collected that year. Fish collected from each station on 24 May 1982 were marked with a subcutaneous latex injection to evaluate movement within the stream. Age was determined by analysis of scale annuli. Relative weights (W_r) (Anderson 1980) were computed using standard weights proposed by Cooper (1961).

Stream morphometry characteristics were measured in July 1982 at each of the five electrofishing stations. Eleven transects perpendicular to the stream bank and spaced 6.1 m apart along each 61-m section of stream were established. Stream width and water depth at 0.15-m intervals across the transect and at both banks were measured. Data from the 11 transects were pooled, and mean depth, width, and depth at stream-bank interface were calculated. Percent of stream canopy coverage at each transect was estimated by assigning numerical values from 1 to 5 corresponding to intervals of stream canopy cover (1 = 81%–100%, 2 = 61%–80%, 3 = 41%–60%, 4 = 21%–40%, 5 = 0%–20%) which shaded the stream surface. Bottom substrate at each station was also examined. A shovel was used to remove three samples of substrate at each station. Samples were air dried, weighed, and sifted through a series of USA Standard Testing sieves. Mean percent by weight of rubble (>76.2/mm), medium/coarse gravel (4.7–76.2/mm), fine gravel (2.0–4.7/mm), coarse sand (1.0–2.0/mm), medium sand (0.5–1.2/mm), and fine sand/silt (<0.5/mm) was calculated for each station.

Analysis of variance was utilized to test for differences in brook trout relative density (number of fishes per 61 m of stream), relative weight (among stations, month, and year), and stream morphometry measurements (among stations). Because the number of brook trout collected at many stations was small, these data were transformed by adding 0.5 to the mean for each station for each date and the square root derived. Following analysis, the transformed data were then squared for presentation of results. Waller-Duncan's K-ratio t-test was employed to define differences. Differences were considered significant at $P \leq 0.05$.

RESULTS

Twelve physicochemical parameters were evaluated on 16 dates from each of the five sampling stations. Variation in precipitation between 1981 and 1984 (Fig. 2) affected water quality between years. Based upon long-term averages from Lead and Spearfish, precipitation in the Black Hills was above normal in 1982, whereas 1981 was a year of lower than normal precipitation. Increased runoff resulted in elevated stream flows throughout the summer of 1982. Mean values for dissolved oxygen and organic phosphorus were significantly higher in 1982 and mean conductivity and pH were significantly lower. Mean fecal coliform number, ammonia nitrogen, and total (Kjeldahl) nitrogen values were higher from all stations in 1982, but these differences were not significant.

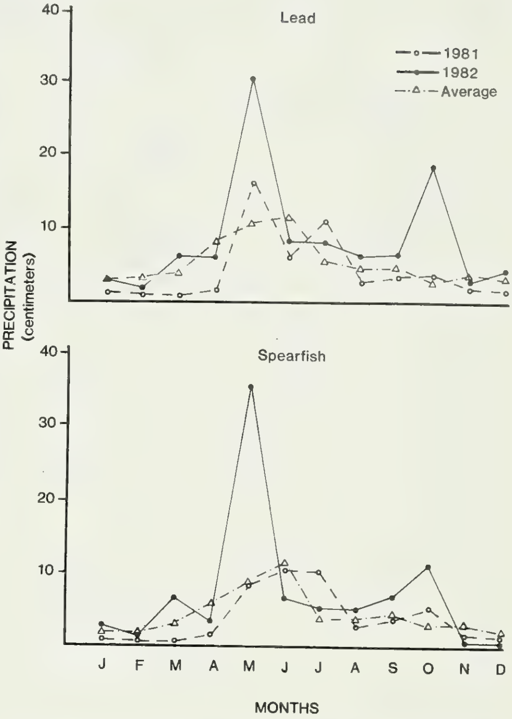

Fig. 2. Monthly precipitation levels for the Lead and Spearfish, South Dakota, gauging stations in the Black Hills during 1981 and 1982.

Seven physicochemical variables differed significantly among stations. Mean turbidity was significantly higher at stations 3, 4, and 5 than upstream at stations 1 and 2 (Table 1). The highest mean turbidity value was at station 3 (35.7 ntu) just below the development site. Mean temperatures at stations 3 and 4 were significantly higher than upstream of stations 1 and 2. Temperature decreased signifi-

TABLE 1. Means of water quality parameters among five stations on Slate Creek.[1]

Variable (Units of measure)	Station 1	2	3	4	5
Turbidity (NTU)	7.1^{a}	3.9^{a}	35.7^{b}	28.4^{b}	26.9^{b}
Temperature (C)	10.1^{a}	9.1^{a}	12.5^{b}	$11.5^{b,c}$	$10.4^{a,c}$
pH	7.5^{a}	7.1^{b}	7.4^{a}	7.5^{a}	7.3^{a}
Conductivity (μmhos)	161.0^{a}	115.4^{b}	163.3^{a}	163.2^{a}	167.6^{a}
Hardness (mg/l $CaCO^3$)	110.3^{a}	82.5^{c}	102.5^{b}	$105.3^{a,b}$	$105.0^{a,b}$
Alkalinity (mg/l $CaCO^3$)	101.2^{a}	81.9^{b}	94.1^{a}	97.8^{a}	100.0^{a}
Fecal coliform (#/100ml)	$173.7^{a,b}$	78.8^{b}	100.2^{b}	$163.9^{a,b}$	309.4^{a}

[1] Means followed by the same superscript for each variable are not different ($P > 0.05$) based on Waller Duncan's K-ratio t-test.

TABLE 2. Numbers and species of fishes collected from Slate Creek and South Slate Creek between June 1981 and August 1982.

	1981				1982			
	June	July	August	$\overline{X}$	May	July	August	$\overline{X}$
Station 1								
Brook Trout	5	2	1	2.7	8	12	6	8.7
White sucker	0	1	0	0.3	0	0	0	0.0
Longnose dace	0	0	0	0.0	0	0	0	0.0
Fathead minnow	0	0	0	0.0	0	0	0	0.0
Station 2								
Brook trout	0	0	0	0.0	5	8	5	6.0
White sucker	0	0	0	0.0	0	0	0	0.0
Longnose dace	0	0	0	0.0	3	0	2	1.7
Fathead minnow	0	0	0	0.0	0	0	0	0.0
Station 3								
Brook trout	7	4	4	5.0	5	5	2	4.0
White sucker	1	2	2	1.3	0	5	1	2.0
Longnose dace	1	2	5	2.7	2	23	23	16.0
Fathead minnow	0	0	0	0.0	0	1	0	0.3
Station 4								
Brook trout	15	44	26	28.3	9	14	19	14.0
White sucker	0	0	0	0.0	0	5	5	3.3
Longnose dace	6	7	2	5.0	1	1	7	3.0
Fathead minnow	0	0	0	0.0	0	0	0	0.0
Station 5								
Brook trout	19	8	20	15.7	12	12	11	11.7
White sucker	7	2	0	3.0	0	10	21	10.3
Longnose dace	14	21	53	29.0	0	6	10	5.3
Fathead minnow	0	0	0	0.0	0	0	0	0.0

cantly from a mean of 12.5 C at station 3 to 10.4 C downstream at station 5. Mean temperature at station 5 was not significantly different from mean values from stations 1 and 2. Conductivity, pH, hardness, and alkalinity were all significantly lower at station 2 than at any of the other stations. Mean total coliform numbers at station 5 were significantly higher than at stations 2 and 3. No significant differences were detected among the five stations for phosphorus (orthophosphate and organic phosphate) or nitrogen (ammonia and organic), but nutrient levels were the highest at stations 4 and 5.

Brook trout, an introduced game species, was the most abundant fish in the study area and was the only species consistently collected at stations both above and below the development site (Table 2). Brook trout composed 53.4% of the fishes collected from the five stations over the two-year period. Other species occurring within the study area were white sucker (*Catostomus commersoni*) (11.3%), longnose dace *(Rhinichthys cataractae*) (35.1%), and fathead minnow (*Pime-phales promelas*) (0.2%).

Differences among stations were observed during both years of the study. Significant dif-

TABLE 3. Mean densities of brook trout per 61m of stream from five stations along Slate Creek during 1981 and 1982.[1]

Year	Station Number 1	2	3	4	5
1981	3.0^{a}	0.5^{a}	$5.4^{a,b}$	28.6^{c}	$15.6^{b,c}$
1982	9.0^{a}	6.4^{a}	4.4^{a}	14.2^{b}	$12.2^{a,b}$

[1] Means followed by the same superscript across rows are not different ($P > 0.05$) from each other based on Waller Duncan's K-ratio t-test.

TABLE 4. Mean values for stream morphometry characteristics among five stations along Slate Creek.[1]

Variable (Units of measure)	Station 1	2	3	4	5
Stream depth (cm)	12.2^{a}	27.9^{b}	14.8^{a}	24.7^{b}	28.1^{b}
Stream-shore depth (cm)	5.5^{a}	$11.4^{a,b}$	5.0^{a}	$19.0^{b,c}$	23.1^{c}
Stream cover (%)	3.6^{a}	5.0^{b}	3.6^{a}	1.8^{c}	3.4^{a}
Fine sand/silt (%)	2.6^{a}	0.7^{a}	29.6^{b}	$11.6^{a,c}$	$22.6^{b,c}$
Stream width (cm)	$93.3^{a,c}$	260.7^{b}	$94.0^{a,c}$	$67.7^{a,c}$	106.7^{c}

[1] Means followed by the same superscript for a variable are not different ($P > 0.05$) from each other based on Waller Duncan's K-ratio t-test.

ferences ($P \leq 0.05$) were observed both among stations and station-year interaction. Due to the interaction observed, data from each year was subjected to a separate analysis of variance. The results indicated that during 1981, fish were most abundant in downstream stations (i.e., 4 and 5). A weaker trend among stations in trout density was observed during 1982, although the highest numbers of brook trout were still collected in the downstream stations (Table 3).

Increases in trout density were generally consistent with increases in mean stream depth and mean depth at the bank (Table 4). During both years brook trout densities below the development site were higher at station 4, which had the greatest summer canopy cover and the lowest amount of sand or silt deposition among downstream stations. Significant differences in stream width among stations did not appear to be related to trout density. Although mean bank depth and mean depth of stream were high at station 2, trout densities were low because flows were not perennial through the 61 m electrofishing section.

Considerable variation in brook trout (relative weight) W_r was observed during the study (Fig. 3). During 1981, when stream flows were low, mean W_r decreased from 95.0 in early June to 79.7 in late August. However, in 1982, when stream flows were higher, W_r declined little during the summer months. Analysis of variance indicated significant ($P < 0.05$) differences in W_r among years, months, and stations. The highest mean W_r values were observed at station 2; the lowest were at station 4.

The brook trout population of Slate Creek consisted primarily of age-class I and II fish; age-class III fish were collected only in 1982 (Fig. 4). The 1980 year-class was the strongest cohort during both years of the study. Recruitment within the study area occurred primarily at station 4 and, to a lesser extent, at station 3. During both years of the study, the numbers of young-of-the-year fish collected were lower than the number of yearlings. Age-class I fish composed that largest portion of that Slate Creek brook trout population at all stations during the study, and were always dominant at stations 1 and 2. No movement of brook trout was observed among stations. Mean recapture rates of fish marked in late May were 41.0% on 1 July and 12.8% on 12 August 1982.

DISCUSSION

Lotic populations of brook trout are typified by short-lived populations (McAfee 1965) inhabiting headwater streams (Neves and Pardue 1983). Brook trout exhibit a high tolerance to environmental variation. Lee and Rinne (1980) observed brook trout, a char, to have a slightly higher tolerance to elevated temperature fluctuation than several other trout species, and Brett (1956) reported that brook trout have a greater cold tolerance than several trout species. In addition, brook trout are also tolerant to extremes to both pH (Daye and Garside 1975) and turbidity (Gradall and Swenson 1982). Tolerance to environmental

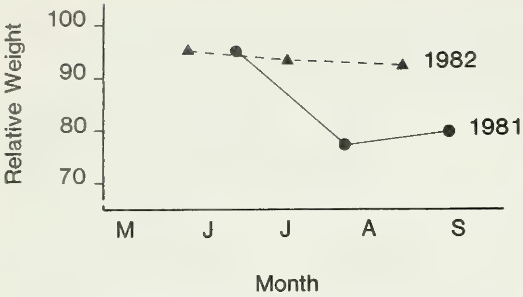

Fig. 3. Mean relative weight (W_r) values for brook trout by month from Slate Creek and South Slate Creek for 1981 and 1982.

change has no doubt led to the success of brook trout stocking within a wide geographical range outside its native distribution (MacCrimmon and Campbell 1969).

Tolerance to changes in water quality results in low sensitivity to some forms of environmental perturbation. In the present study, brook trout were poor indicators of the observed changes in turbidity, temperature, and nutrient loading. Natural fish populations have been considered inferior to macroinvertebrate communities as water quality indicators even though individual fish species have been successfully utilized in bioassays (Price 1979). However, several researchers (e.g., Binns and Eiserman 1979, Raleigh 1982, Parsons et al. 1981) have studied the importance of physical characteristics of streams in determining trout density. Brook trout densities in the present study were responsive to changes in physical characteristics of the stream, particularly stream flow, mean stream depth, depth at the bank, and canopy cover—the major components of cover in a small stream. Both Stewart (1970) and Hunt (1971) similarly reported that depth and cover were dominant factors affecting brook trout densities in streams. Fraley and Graham (1981) observed that cover, substrate, and depth were the primary factors among 30 physical habitat characteristics measured that best predicted densities of cutthroat trout (*Salmo clarki lewisi*) and bull trout (*Salvelinus confluentus*).

Relative weights were higher for brook trout during 1982, when high precipitation resulted in a greater quantity of drift organisms available (Drewes 1984). The relationship of W_r to stations was probably due to intraspecific competition, with the lowest values occurring at the station with the highest relative density of trout. Condition of trout, as expressed by W_r, was also influenced more by natural variation than water quality.

As primary components of the ichthyofauna in headwater mountain streams, brook trout represent one of the initial biotic components impacted by nonpoint sources of watershed disruption. Because of their tolerance to changes in the water medium, brook trout are not good indicators of moderate alterations in water quality. Brook trout appear to be sensitive to changes in stream morphometry and should be adequate indicators of physical disruptions within streams.

ACKNOWLEDGMENTS

Funding for the project was provided by the U.S. Forest Service through an Eisenhower Consortium grant and project funds from the Rocky Mountain Forest and Range Experiment Station. Thanks are expressed to Brian Smith, Michele Deisch, and Larry Beagle for assisting in field collection and to Dr. Charles G. Scalet, Dr. Lester D. Flake, Ron Koth, and Dick Ford for reviewing this manuscript.

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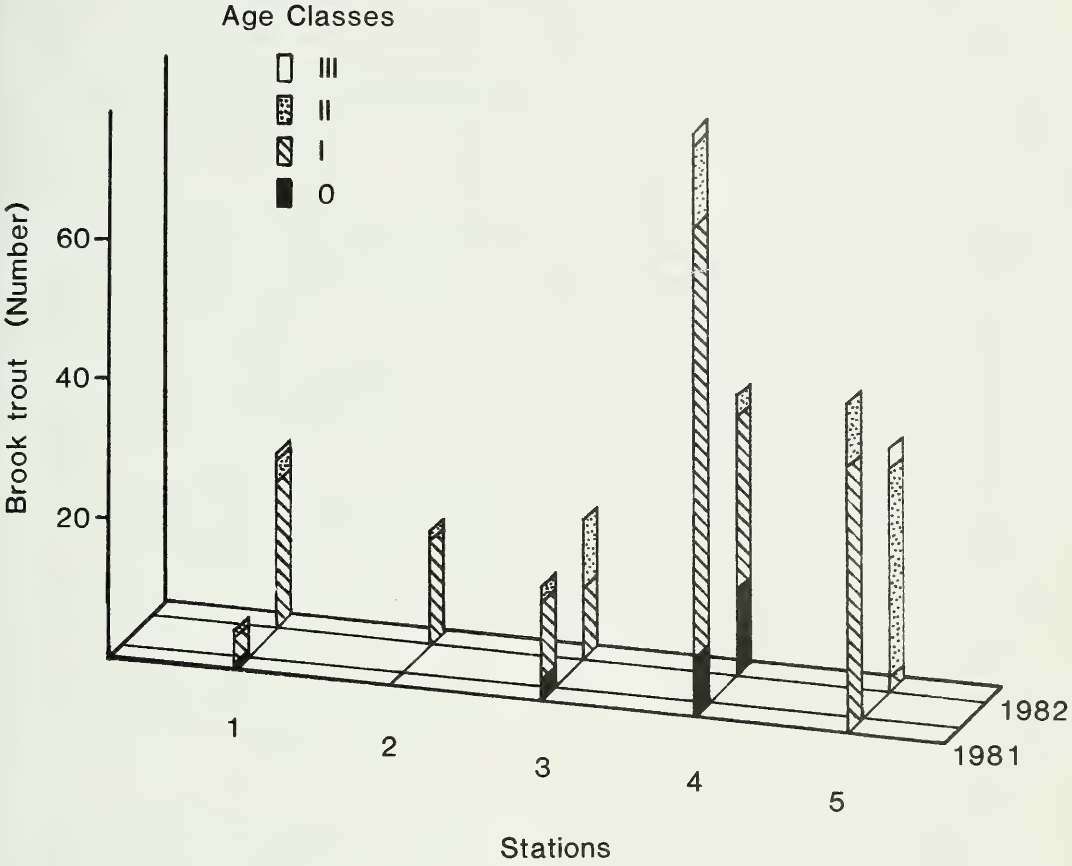

Fig. 4. Age distribution and abundance of brook trout among stations from the Slate Creek study during 1981 and 1982.

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FLORISTIC ANALYSIS OF THE SOUTHWESTERN UNITED STATES

Steven P. McLaughlin[1]

ABSTRACT.—A study was made of the distributions of native, terrestrial, vascular plants occurring in 50 local floras from throughout the Basin and Range and Colorado Plateau physiographic provinces of the southwestern United States. The objectives of the study were to objectively define and describe the floristic elements—assemblages of species with roughly coincident geographic distribution—occurring in the southwestern United States and to determine what such assemblages reveal about the floristic history of the region.

The total flora (native, terrestrial species only) of the Southwest is estimated at 5,458 species, 77% of which were recorded in 1 or more of the local floras. Nearly 22% of these species are endemic to the study region. A majority of the species were found to be relatively rare. The average range of a species included only 4 floras, and 90% of the species were recorded from 11 or fewer floras; only 81 species (1.5%) were recorded from 50% or more of the floras. Trees constitute 2% of the regional flora and have the widest average distribution; perennial herbs constitute 59% of the flora and have the most restricted distributions.

Factor analysis was used to identify seven floristic elements for the region: a Great Basin element, a Mojavean element, a Colorado Plateau element, a Chihuahuan element, an Apachian element, and a Mogollon element. This factor analysis solution was shown to satisfy criteria of interpretability and consistency. The Mojavean, Colorado Plateau, and Apachian elements are believed to be autochthonous. The other four elements show high overlap in species composition with one or more adjacent regions.

Each floristic element is mapped to show its geographic form and distribution. Analysis of these maps shows how the existence of objectively defined floristic elements is not contradictory to either the individualistic view of the distribution of a species or local continuity of vegetation and flora.

The rarity of the majority of species and the clear association of floristic elements with rather narrowly circumscribed Holocene environments suggests that many Southwestern species have migrated little and are of rather recent, probably postglacial origin. Geographic "principles" derived from the distribution patterns of relatively few, widespread, dominant, usually woody species may not be applicable to entire, regional floras.

Plant geographers have long recognized that plant species can be grouped on the basis of similarities among their geographic distributions. Such floristic groups have generally been termed "geographical elements" by European phytogeographers (Stott 1981, Cain 1947). The same concept is embodied in such terms as "natural floristic areas" (Raup 1947), "floristic assemblage" (Cain 1944), "floristic group" (Gleason and Croquist 1964), "areal types" (Whittaker and Niering 1964), "categories of geographic origin" (Stebbins 1982), or "directional classes" (Meyer 1978) of American authors. The term *element* is used uncritically in the American literature as a synonym for taxon or taxa.

A concept related to that of floristic assemblages is that of floristic or biotic provinces. Provinces in the sense of Dice (1943) are reasonably discrete areas with characteristic physiography, climate, vegetation, flora, and fauna. There may be a one to one correspondence between floristic groups and floristic provinces (e.g., Gleason and Cronquist 1964), in which case the floristic group is the characteristic flora of the floristic province. More often floristic groups are conceived as assemblages of variable and often overlapping areal extent, including a few wide-ranging types and many more narrowly defined types. A good example is the set of "areal types" used by Whittaker and Niering (1964) in their analysis of the flora of the Santa Catalina Mountains of southern Arizona. Included are widespread and overlapping "temperate," "western," "northern," and "southwestern" types along with more restricted and largely discrete "Sonoran," "Rocky Mountain," "Plains," "Madrean," and "Chihuahuan" types.

This chaos in terminology regarding floristic assemblages is a consequence of the inadequate empirical and theoretical basis for such concepts in the American tradition. Gleason (1926) challenged the validity of the organismic concept of associations as applied to vegetation by F. E. Clements and argued further that each species has its own individualistic environmental requirements and migrational history. It should follow, therefore, that each community of species is unique and any attempt to identify repeatable associations must be highly subjective. The "individualistic concept" and the related "continuum concept" have been accepted by most American plant ecologists (McIntosh 1967).

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The ideas of Gleason were very broadly applied to plant geography by Mason (1947) and Cain (1944, 1947). Mason (1947) invoked the individualistic nature of the species and the principles of past migrations of species (as revealed in the fossil record) to argue against the existence of persistent and recognizable floras. Cain (1947) believed that floristic elements could be recognized only relative to the particular area under investigation and not as a universal system of floristic regions. He linked the ideas of floristic groups and plant association types, and went on to argue against the objective recognition of association types, implicitly casting doubt on the objective recognition of floristic assemblages of any form.

The current attitude toward floristic assemblages is well illustrated in a statement by Johnston (1977:356):

> "Recurrent distribution patterns" may simply be the result of intuitive (but in this case unfortunate?) tendencies to lump and generalize, in the way the eye tends to connect totally unrelated star-clusters into meaningless but "recognizable" patterns in the night sky.

A recent text on biogeography (Brown and Gibson 1983) discusses the association/continuum conflict but makes no reference to the problem of floristic elements.

If each plant species is uniquely and independently distributed, and therefore recognition of floristic assemblages must be inherently arbitrary and subjective, why have so many phytogeographers nevertheless recognized such groups? Can phytogeographical elements be described more objectively and, if so, how can they be reconciled with individualistic concepts and what do they mean in terms of the evolutionary histories of their species? The objective of this paper is to answer these questions through a floristic analysis of vascular plant distributions recorded in local floras from the southwestern United States.

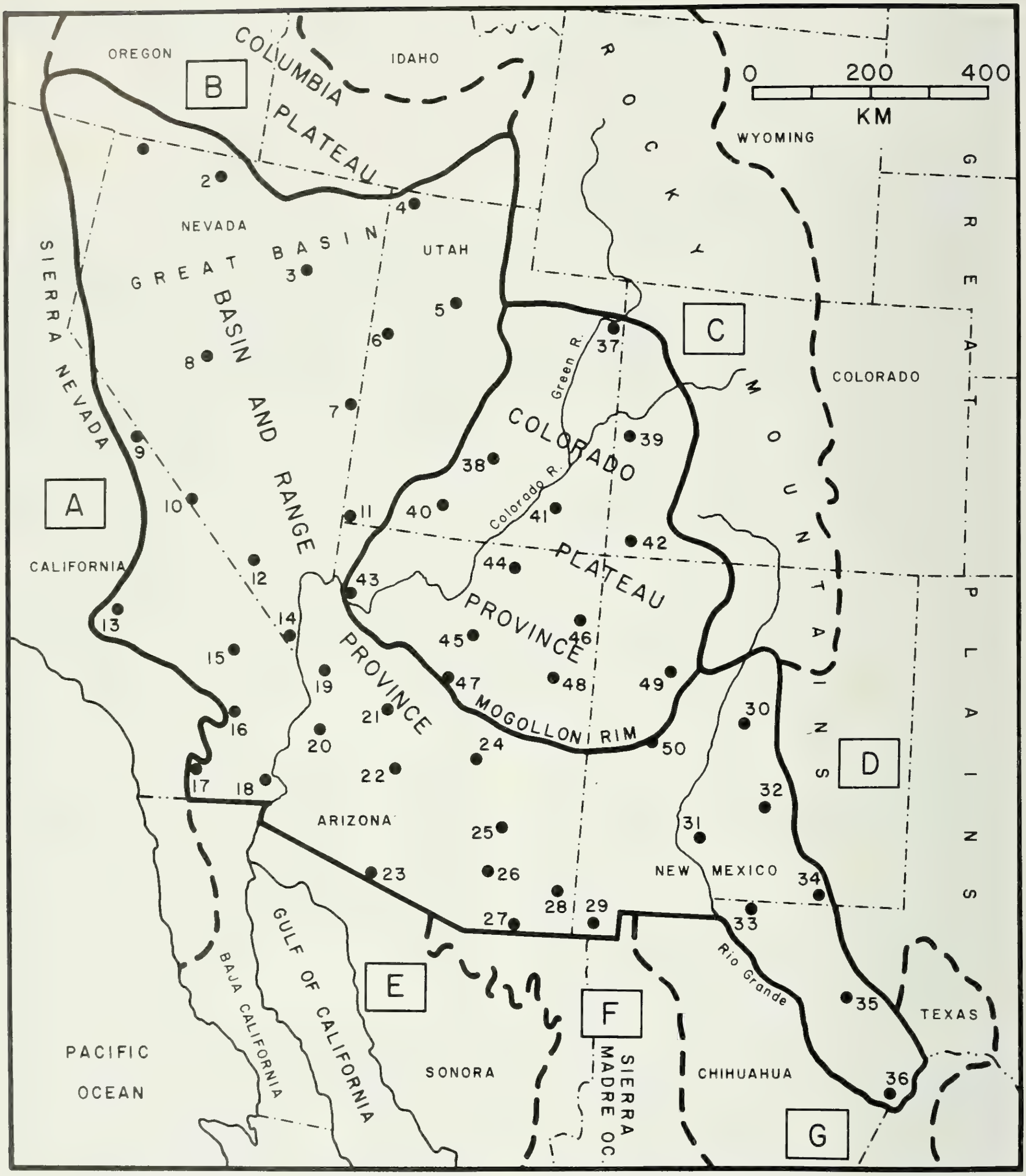
Methods

Study Region

The study region includes the Colorado Plateau Physiographic Province and the Basin and Range Physiographic Province north of the U.S.-Mexico International Boundary, both as mapped by Hunt (1967) (Fig. 1). This region is bounded by the Sierra Nevada and southern California transverse ranges on the west; by the Columbia Plateau on the north; and by the Rocky Mountains and southern Great Plains on the east. Only the southern boundary is artificial. This region will be referred to simply as the Southwest.

The majority of the region lies between the two great Western mountain systems—Sierra Nevada on the west and Rocky Mountains to the east. The entire region is arid to semiarid. The Great Basin section of the Basin and Range Province experiences hot summers, cold winters, and mostly winter precipitation. The southeastern portion of the Basin and Range Province is at the opposite end of the climatic spectrum for the region, with hot summers, mild winters, and mostly summer precipitation. The most arid portion of the region centers around the lower Colorado River Valley.

The study region has generally been recognized as a natural one by biogeographers. One of the earliest formal treatments is that of Dice (1943) and a recent one is that of Cronquist (1982). Both recognize a semiarid natural region lying between the Sierra Nevada and the Rocky Mountains that extends into northern Mexico. Cronquist's Great Basin Province essentially includes Dice's Artemisian and Navahonian provinces; Cronquist's Sonoran Subprovince is composed of Dice's Mohavean and Sonoran provinces; and their Chihuahuan regions are similar. The principal difference is that there is nothing in Cronquist's treatment that corresponds closely to Dice's Apachian Province of the uplands of southeastern Arizona, southwestern New Mexico, and northwestern Sonora.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NEVADA
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BASIN AND RANGE PROVINCE
SIERRA NEVADA
A
CALIFORNIA
C
COLORADO
Green R.
Colorado R.
COLORADO PLATEAU PROVINCE
MOGOLLON RIM
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ARIZONA
NEW MEXICO
TEXAS
Rio Grande
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CHIHUAHUA
SIERRA MADRE OC.
PACIFIC OCEAN
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GULF OF CALIFORNIA
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Fig. 1. Map of study region, Southwestern United States. Numbers refer to local floras listed in Table 1; letters in boxes refer to peripheral regions listed in Table 6.

Data Base

Fifty local floras from the Southwest were examined (Table 1). These floras represent a systematic sample of the regional southwestern flora and were selected to provide as thorough and uniform coverage of the study region as possible (see Fig. 1).

Complete bibliographic citations for 33 of the 50 local floras can be found in Bowers' (1982) annotated bibliography. Flora 42 is based both on the publication referenced in Bowers (1982) and on an unpublished checklist distributed by Natural Bridges National Monument. Flora 13 consists of those plants listed by Twisselman (1967) as occurring in

TABLE 1. Southwestern local floras used in floristic analysis. Map numbers refer to map locations in Figure 1.

Map location	Flora designation	Number of species	Reference
1	Sheldon National Wildlife Refuge	489	Rogers & Tiehm (1979)
2	Santa Rosa Mountains	318	Bowers (1982)
3	Ruby–East Humboldt Mountains	507	Lewis (1971)
4	Raft River Mountains	295	Bowers (1982)
5	Stansbury Mountains	476	Taye (1983)
6	Deep Creek Mountains	395	Bowers (1982)
7	Wheeler Peak area	380	Bowers (1982)
8	Toiyabe Mountains	440	Bowers (1982)
9	White Mountains (California-Nevada)	677	Lloyd & Mitchell (1973)
10	Grapevine Mountains	463	Kurzius (1981)
11	Beaver Dam Mountains	489	Bowers (1982)
12	Spring Range (Charleston Mountains)	603	Bowers (1982)
13	Eastern Kern County	368	Twisselman (1967)
14	Newberry Mountains	385	Holland (1982)
15	Granite Mountains	376	Thorne et al. (1981)
16	Joshua Tree National Monument	534	National Park Service (1973)
17	Western Colorado Desert Region	441	Clemons (1984)
18	Eastern Imperial County	227	McLaughlin & Bowers (unpublished)
19	Hualapai Mountains Planning Unit	623	Bowers (1982)
20	Harcuvar Planning Unit	491	Bowers (1982)
21	Skull Valley Planning Unit	488	Bowers (1982)
22	White Tank Mountains	304	Bowers (1982)
23	Organ Pipe Cactus National Monument	477	Bowers (1982)
24	Sierra Ancha Experimental Forest	655	Bowers (1982)
25	George Whittell Wildlife Preserve (Aravaipa Canyon)	398	Bowers (1982)
26	Saguaro National Monument, Rincon Mountain Unit	799	Bowers (unpublished)
27	Mule Mountains	387	Wentworth (1982)
28	Chiricahua National Monument	619	Bowers (1982)
29	Animas Mountains	620	Bowers (1982)
30	Manzano Mountains	349	Bowers (1982)
31	Jornado Experimental Range	493	Bowers (1982)
32	White Mountains (New Mexico)	895	Bowers (1982)
33	Hueco Tanks State Park	315	Worthington (1980)
34	Carlsbad Caverns—Guadalupe Mountains	543	Bowers (1982)
35	Davis Mountains	461	Sikes and Smith (1975)
36	Big Bend National Park	751	Warnock (1967)
37	Dinosaur National Monument	304	Bowers (1982)
38	Capitol Reef National Monument	402	Bowers (1982)
39	Colorado National Monument	302	Bowers (1982)
40	Bryce Canyon National Park	402	Buchanan & Graybosch (1982)
41	Natural Bridges National Monument	298	Bowers (1982), National Park Service (no date)
42	Mesa Verde	333	Bowers (1982)
43	Lower Grand Canyon area	250	Bowers (1982)
44	Navajo National Monument	252	Bowers (1982)
45	Wupatki National Monument	178	Bowers (1982)
46	Canyon de Chelly National Monument	396	Bowers (1982)
47	Oak Creek Canyon and vicinity	507	Bowers (1982)
48	Petrified Forest National Park	277	Bowers (1982)
49	Mount Taylor	274	Bowers (1982)
50	Datil Mountains	483	Bowers (1982)

the arid shrub, creosote bush, and shadscale scrub portions of eastern Kern County, California. Flora 17 consists of those plants listed by Clemons (1984) as occurring in the Vallecito, Carrizo, and Borrego floristic areas of eastern San Diego County, California. Floras 18 and 26 are from projects in progress.

The number of species listed in these local floras varies from a low of 178 to nearly 900 species. The species numbers given in Table 1 are in every case lower than the numbers given in the original reports, since several classes of species were not included in the present analysis:

a. Introduced species.
b. Strict aquatics, i.e., floating, submerged, and emergent plants of permanent lotic habitats (ponds, lakes, reservoirs, cattle tanks, etc.)
c. Synonyms at the species level.
d. Species listed by authors as "likely" to occur in their areas.

Aquatic species were excluded because of their limited value in comparative geographic studies. Such species tend to be very widespread but are relatively uncommon in dry regions, depending on the occurrence of suitable (often man-made) habitats. Kartesz and Kartesz (1980) and Welsh et. al (1981) were used to achieve consistency and uniformity in nomenclature and to identify synonymous plant names. In the remainder of this paper, flora of the study region will refer to the native, vascular, terrestrial flora as defined above.

In addition to recording the presence of species in each of the 50 local floras, manuals and checklists for the region (Holmgren and Reveal 1966, Cronquist et al. 1972, 1977, 1984, Kearney and Peebles 1969, Martin and Hutchins 1980, Munz 1968, Correll and Johnston 1970) were consulted to determine what additional species occur in the Southwest. Finally, again using regional manuals, I recorded occurrences of all southwestern species in each of seven adjacent or peripheral regions (see Fig. 1): (A) Pacific region (roughly equivalent to the California floristic province), (B) Columbia Plateau, (C) Rocky Mountain region, (D) Great Plains, (E) Sonoran Desert region, (F) Sierra Madre region, taken here as the area in northern Mexico between the Sonoran and Chihuahuan deserts, and (G) Chihuahuan Desert region. The resulting lists of southwestern species occurring in these peripheral regions were used as floras in the data analysis (see below) to examine the relationships between the Southwest flora and that of the peripheral regions, and to distinguish allochthonous from autochthonous elements.

Data Analysis

Similarities in the species composition of the 50 local floras and seven peripheral regions were examined using factor analysis. Factor analysis is a family of ordination techniques used to examine the pattern and structure of large data matrices. Factor analysis has long been used in sociological and geographic studies, and its applications for plant ecology have been discussed by Goodall (1954) and for phytogeography by Jardine (1972). Since it is essentially a nonhierarchical clustering procedure, factor analysis is a particularly appropriate tool for examining floristic affinities (Jardine 1972).

Factor analyses are of two basic types. Consider a matrix that lists the presences of s species (rows) in n floras (columns). A Q-mode analysis would examine the relationships in an s x s matrix of correlations or similarities among the s species; an R-mode analysis would examine the relationships in an n x n matrix of correlations or similarities among the n floras. Ideally one would prefer to perform a Q-mode analysis to investigate floristic affinities, but two problems arise: there is no suitable coefficient or similarity index available to correlate species ranges *when most of the species are very rare*; and available factor analysis programs are limited to ~100 variables (species in this case), a number smaller than the smallest local flora used in this study.

I therefore used an R-mode analysis based on similarity indices among the floras and peripheral regions. The R-mode and Q-mode solutions should agree whenever clear-cut patterns actually exist in the data (Bryant et al. 1974). The similarity index used was that of Otsuka (as given in Simpson 1980):

$$IS_{Otsuka} = C_{ij} / (A_i B_j)^{1/2}$$

where:

A_i = number of species in flora i;
B_j = number of species in flora j;
C_{ij} = number of species common to floras i and j.

Since IS_{Otsuka} can take only positive values between 0 and 1, the analysis used here is, in the terminology of Pielou (1984), one using standardized but noncentered data. With data in this form, the first several factors are usually unipolar, i.e., all or nearly all the factor loadings (see below) are of the same sign, all positive or all negative. Furthermore, there are as many unipolar factors as there are qualitatively different clusters of data points (Pielou 1984).

Table 2. Statistical summary of the native, terrestrial flora of the Colorado Plateau and Basin and Range provinces of the southwestern United States.

Taxonomic group	Families	Genera	Species	Endemic species no.	Endemic species %
Ferns and fern allies	9	24	120	3	(2.5)
Gymnosperms	3	7	36	2	(5.6)
Monocotyledons	10	136	723	63	(8.7)
Dicotyledons	105	827	4579	1119	(24.4)
Totals	127	994	5458	1187	(21.7)

The factoring program used was that of Nie et al. (1975). I used principal components factor extraction with orthogonal (varimax) rotation, probably the most commonly used factoring technique in ecological studies. Several aspects of the analysis were altered later to check on the consistency of the solution (see below).

Results

Description of the Flora

The flora of the study region is summarized in Tables 2–6. A total of 4,185 species were recorded from the 50 local floras; 1,273 additional species native to the study region were identified from the literature. The estimated total regional flora (5,458 species) is probably somewhat conservative, since the flora of the intermountain region in Utah and Nevada is still being compiled and monographed. The sample of species in the 50 local floras, however, probably represents at least 70%–75% of the regional flora.

Table 2 lists total species and endemic species by major taxonomic group. Within the study region, 21.7% of the species are endemic. Most of the endemic species are dicotyledons, and, in fact, nearly a quarter of the dicotyledons are endemic. The proportion of endemics in the study region is much lower than that in the California floristic province to the west (47.7%) but higher than that of other continental areas including Alaska (5.9%), Texas (9.0%), or the northeastern United States (13.5%) (Raven and Axelrod 1978). There is a rather high ratio of species per genus (5.5) in the Southwest, similar again to that of the California floristic province (5.6) and higher than for most other continental areas (3.0–4.0) (Raven and Axelrod 1978).

The most common families and genera within the study region are listed in Table 3. Commonness as used in this paper refers to ubiquity rather than abundance (Preston 1948), although ubiquitous taxa are also usually abundant (Hengeveld and Haeck 1982, Brown 1984). The Asteraceae, which is the largest family, accounting for 17.1% of the total species in the flora, is also the most common family, with 78.6 species/flora. Poaceae is the second most common family even though it is represented by more than 100 fewer species than the Fabaceae, the third most common family. The families Fabaceae, Brassicaceae, Scrophulariaceae, Boraginaceae, Polygonaceae, and Cactaceae are characteristic families of the region in that they have both a large number of species and a high proportion (>25%) of their species endemic within the region. The five most common genera—*Eriogonum, Astragalus, Cryptantha, Penstemon*, and *Phacelia*—also have a high proportion of endemic species. Several large genera common within but not characteristic of the region, including *Carex, Juncus*, and *Salix*, are mostly found in relatively mesic habitats.

The frequency distribution for the 5,458 species occurring in the Southwest is shown in Figure 2. The average number of floras per species is 4.07. Only 81 species (1.5%) were recorded from one-half or more of the local floras (Table 4). Most of these widespread species have several subspecific taxa within the region, indicating that they are genetically variable species. The widespread species listed in Table 4 are found throughout most of western North America. The vast majority of species in the region, however, are rare. Nearly two-thirds of the species are recorded from three or fewer floras.

The distribution patterns of southwestern species, as revealed by their occurrence in the 50 local floras examined, are probably reliable evidence for the rarity of most species in this

TABLE 3. Commonest families and genera of native, terrestrial plants in the Colorado Plateau and Basin and Range provinces.

Taxon	Total species	Species per flora	Endemic species number	Endemic species %
10 MOST COMMON FAMILIES:				
Asteraceae	932	78.6	213	(22.9)
Poaceae	359	42.5	22	(6.1)
Fabaceae	493	28.2	154	(31.2)
Brassicaceae	208	16.6	66	(31.7)
Scrophulariaceae	276	16.3	114	(41.3)
Boraginaceae	161	13.2	52	(32.3)
Polygonaceae	172	12.8	73	(42.4)
Polemoniaceae	144	11.8	37	(25.7)
Rosaceae	110	11.2	23	(20.9)
Cactaceae	111	9.7	33	(29.7)
20 MOST COMMON GENERA:				
Eriogonum	120	9.4	64	(53.3)
Astragalus	189	7.4	111	(58.7)
Cryptantha	79	6.0	39	(49.9)
Penstemon	118	5.3	70	(59.3)
Phacelia	77	5.2	35	(45.5)
Carex	97	5.0	3	(3.1)
Muhlenbergia	48	4.8	7	(14.6)
Opuntia	36	4.7	7	(19.4)
Erigeron	72	4.7	29	(40.3)
Artemisia	22	3.8	1	(4.5)
Juncus	26	3.8	0	(0)
Chamaesyce	40	3.6	6	(15.0)
Senecio	50	3.6	9	(18.0)
Gilia[1]	46	3.5	14	(30.4)
Bouteloua	19	3.4	1	(5.2)
Brickellia	36	3.4	12	(33.3)
Oenothera[2]	29	3.3	6	(20.7)
Castilleja	45	3.2	13	(28.9)
Lupinus	57	3.2	13	(22.8)
Salix	28	3.2	1	(3.6)

[1] Excluding *Ipomopsis*, *Leptodactylon*.

[2] Excluding *Calyophus*, *Camissonia*.

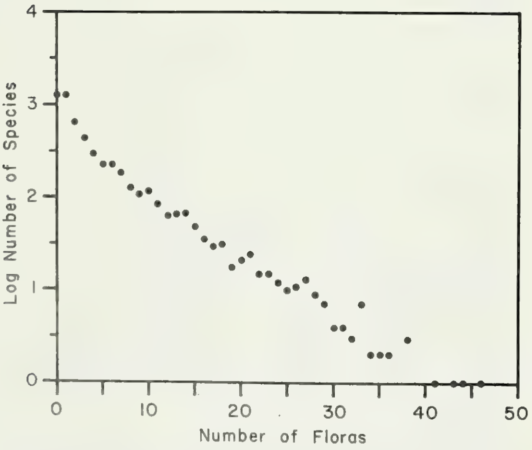


Fig. 2. Frequency distribution showing numbers of species occurring in 0–50 local floras from the southwestern United States.

region. Although I use the term *local* in reference to the floras, most of the floras used in this analysis cover rather extensive areas. Many of the floras are for small to large mountain ranges, national parks, and other areas that encompass a diversity of habitats. Within the boundaries covered by each flora there undoubtedly occur habitats suitable for many species not known to occur in the floras. Even if every species occurred on the average in one additional flora, it would not greatly change the statistics of species distributions; yet it would increase the size of each local flora by ~110 species. It is unlikely that 100 species (on the average) could be added to each local flora, even through very extensive further collection.

The composition of the flora by life form is summarized in Table 5. Trees and shrubs, though widely distributed, constitute only 14.2% of the total flora. Cacti and succulents

TABLE 4. Most commonly encountered species in 50 local floras from the southwestern United States.

Species[1]	Subspecific taxa[2]	% of floras
Artemisia ludoviciana	7	92
Sitanion hystrix	2	88
Descurainia pinnata	12	86
Rhus trilobata	6	82
Erigeron divergens	2	76
Atriplex canescens	3	76
Aristida purpurea[3]	4	76
Gutierrezia sarothrae	2	72
Mentzelia albicaulis	2	72
Poa fendleriana	3	70
Mimulus guttatus	6	70
Vulpia octoflora	3	68
Salix exigua	0	68
Conyza canadensis	3	66
Linum lewisii	3	66
Oenothera caespitosa	8	66
Bouteloua curtipendula	2	66
Senecio douglasii	3	66
Oryzopsis hymenoides	2	66
Holodiscus dumosus	2	66
Chrysothamnus nauseosus	20	64
Lappula redowskii	2	64
Sporobolus cryptandrus	0	64
Opuntia phaeacantha	10	62
Sporobolus airoides	0	62
Stephanomeria pauciflora	2	62
Echinocereus triglochidiatus	8	62
Helianthus annuus	0	60
Leucelene ericoides	0	60
Erioneuron pulchellum	0	60
Rosa woodsii	4	60
Cercocarpus montanus	7	58
Populus fremontii	2	58
Erigeron pumilus	6	58
Draba cuneifolia	3	58
Allionia incarnata	0	58
Bouteloua gracilis	2	58
Castilleja chromosa	2	58
Artemisia dracunculus	2	56
Brickellia californica	2	56
Symphoricarpos oreophilius	2	56
Astragalus lentiginosus	37	56
Plantago patagonica	3	56
Agropyron trachycaulum	4	56
Populus tremuloides	0	56
Comandra umbellata	3	56
Castilleja linearifolia	0	56
Achillea millefolium	11	54
Ceratoides lanata	2	54
Chenopodium fremontii	2	54
Juncus arcticus[4]	3	54
Phoradendron juniperinum	2	54
Mirabilis multiflora	3	54
Bromus carinatus[3]	0	54
Koeleria cristata	0	54
Ipomopsis aggregata	4	54
Amelanchier utahensis	2	54
Datura inoxia	0	54
Celtis reticulata	0	54
Baccharis glutinosa	0	52
Senecio multilobatus	0	52
Cryptantha pterocarya	4	52
Erysimum capitatum	6	52
Lepidium lasiocarpum	4	52
Aristida adscensionis	3	52
Juncus ensifolius[3]	2	52
Ranunculus cymbalaria	3	52
Nicotiana trigonophylla	0	52
Chrysothamnus viscidiflorus	5	52
Pinus ponderosa	3	50
Pseudotsuga menziesii	2	50
Gutierrezia microcephala	0	50
Amaranthus blitoides	0	50
Artemisia tridentata	3	50
Stipa comata	2	50
Gilia sinuata	0	50
Clematis ligusticifolia	3	50
Fallugia paradoxa	0	50
Salix gooddingii	0	50
Physalis hederifolia	2	50
Verbena bracteata	0	50

[1] Nomenclature follows Kartesz and Kartesz (1980) except where otherwise footnoted.
[2] Number of subspecific taxa listed in Kartesz and Kartesz (1980).
[3] *sensu* Cronquist et al. (1977).
[4] *sensu* Hultén (1968).

(mostly Agavaceae) make up 3.3% of the flora; annuals constitute 23.5%, a relatively high proportion. Perennial herbs, by far the largest group (58.9%), are the least widely distributed of the life forms listed in Table 5. Among herbaceous plants, species of Poaceae are relatively widespread (5.9 floras/species). Many species of the large genera characteristic of the region are rather uncommon, e.g., *Astragalus* (2.0 floras/species), *Penstemon* (2.2 floras/species), *Cryptantha* (3.1 floras/species), *Erigeron* (3.2 floras/species), *Phacelia* (3.4 floras/species), and *Gilia* (3.8 floras/species).

The number of southwestern species extending into the seven peripheral regions are listed in Table 6. These numbers imply nothing about directions of migration; rather they show only the overlap in species composition between the Southwest and adjacent regions. A species occurring in the Southwest and another region(s) may be: primarily southwestern, barely entering the peripheral region(s); primarily distributed in the peripheral region(s), barely entering the Southwest; or common in both the Southwest and one or more peripheral regions. The greatest overlap

TABLE 5. Summary of flora by life form.

Life form	No. species	Floras/Species
Trees	109	8.79
Shrubs	667	4.92
Perennial herbs	3,217	3.65
Annual herbs	1,285	4.24
Cacti and succulents	180	4.09
Total	5,458	4.06

TABLE 6. Species shared between Southwest and adjacent regions. Letters refer to map locations in Figure 1.

	Species occurring in Southwest	
Peripheral region	Number	Percent of total
A. Pacific region	1,544	28.3
B. Columbia Plateau region	1,224	22.4
C. Rocky Mountain region	1,479	27.1
D. Great Plains region	1,297	23.8
E. Sonoran region	847	15.5
F. Sierra Madre region	1,215	22.3
G. Chihuahuan region	1,119	20.5

occurs with the Pacific peripheral region, the least with the Sonoran Desert peripheral region. Two types of species appear to account for much of the overlap: species of disturbed or weedy habitats, and species of relatively mesic habitats.

Factor Analysis Solution

In principal components analysis the n variables are expressed in terms of n principal components (factors). By convention, only those factors with eigenvalues >1 (i.e., those factors accounting for at least 1/n of the variation in the data) are retained for rotation to the final solution. Nine such factors were extracted in this analysis. The 8th and 9th factors were bipolar with eigenvalues ~1 and could not be simply interpreted. The 1st through 7th factors are depicted in Figures 3–9; they account for 55.4% of the variation in the data.

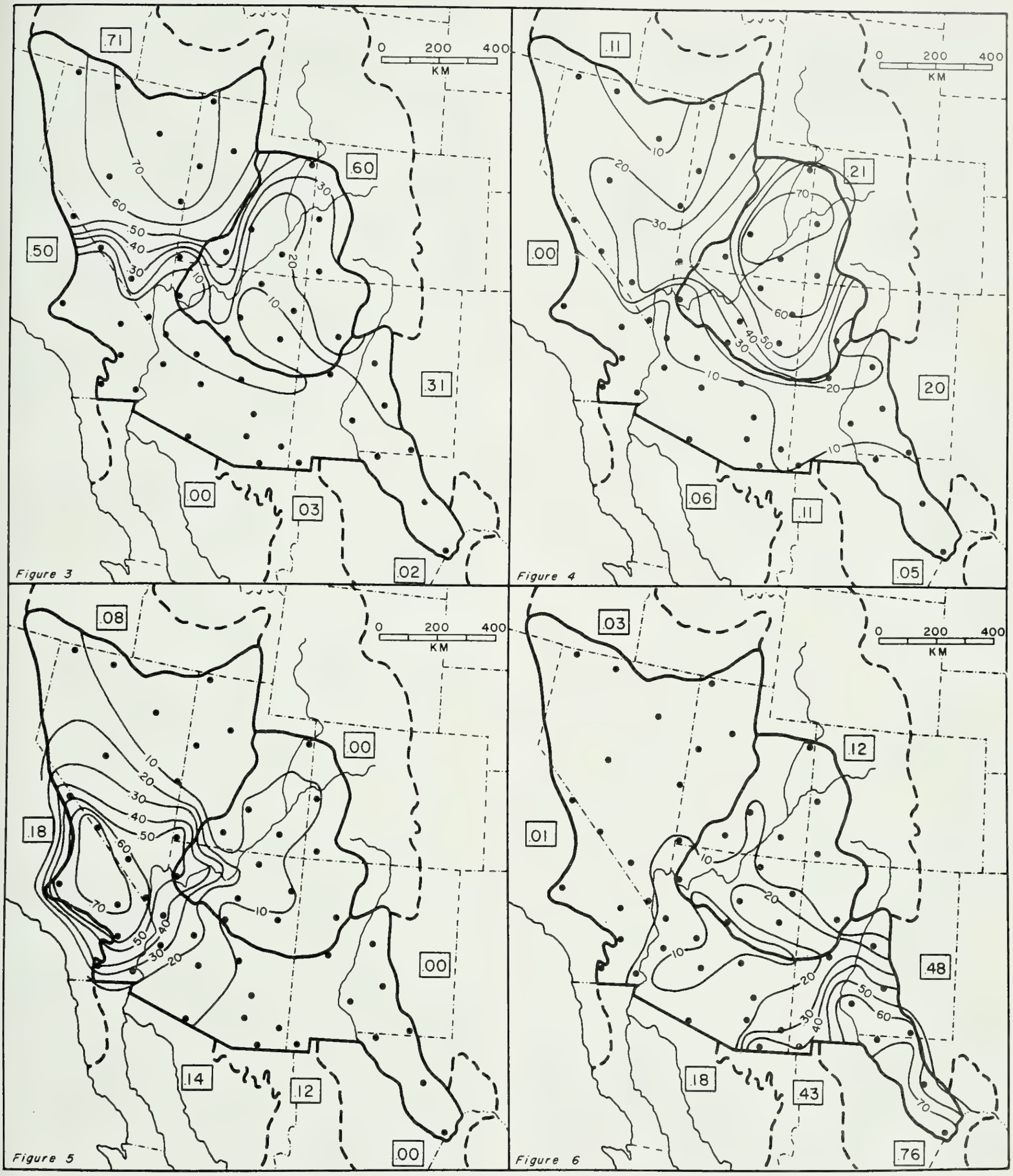
The maps of Figures 3–9 were prepared by plotting the factor loadings for each flora and drawing contours or isolines to show areas of approximately equal factor loadings. Factor loadings are the correlations between the floras and the factors. For this particular analysis, the factor loadings can be interpreted as similarity indices between the floras and the factors. The loadings for the peripheral regions are shown in the boxes on Figures 3–9.

Factor analysis to date has not been used extensively in biogeography, despite its potential ability to simplify complex data sets. Apparently, a major reason for this is that both authors and readers often must engage in some rigorous mental gymnastics to interpret the "meaning" of factors when there is considerable sampling error in the data or when patterns among the variables are in fact weak. Compared to most kinds of ecological data, there is relatively little error in determining which species occur in a particular area of limited extent. If the results of the factor analysis can be mapped, the interpretation should be straightforward—either there are simple, reasonable, and easily understood geographical patterns associated with each factor or there are not.

The factors mapped in Figures 3–9 are geographically meaningful. Each shows high similarity with relatively few adjacent local floras. From these centers of high similarity, the magnitude of factor loadings declines more or less continuously in all directions. In form the mapped factors are reminiscent of the "noda" of Poore (1955). Each factor is most strongly represented in a single section of the study region, and these areas are fairly well delimited. The factors clearly identify what areas within the Southwest show higher than average overlap in species composition between local floras. It seems to me that these seven factors can be interpreted readily as seven floristic elements in the traditional sense, that is, as clusters or centers of roughly coincident species ranges.

Most of the seven floristic elements correspond to natural areas that have been recognized in the past on more subjective grounds. I will discuss each briefly before proceeding to a discussion of the conceptual and theoretical basis for recognizing floristic elements.

1. GREAT BASIN ELEMENT.—Factor 1 (Fig. 3) has high loadings with floras in the Great Basin section of the Basin and Range physiographic province. This element shows a distinct representation in the eastern portion of the Colorado Plateau as well as a recognizable extension into the Mogollon Rim area of central Arizona. The element declines in importance most rapidly toward the south in southern Nevada. Beatley (1975) discusses the topographic and climatic factors in this latter area that are correlated with the transition from Great Basin to Mojave Desert vegetation.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Figs. 3–6: 3, Plots of loadings for factor 1—Great Basin floristic element. 4, Plot of loadings for factor 2—Colorado Plateau floristic element. 5, Plot of loadings for factor 3—Mojavean floristic element. 6, Plot of loadings for factor 4—Chihuahuan floristic element.

The Great Basin element is strongly correlated with the flora of the Columbia Plateau peripheral region to the north. Both are regions of sagebrush desert and conifer-forested mountain ranges. The Great Basin element is also strongly correlated with the Rocky Mountain region to the east and the Pacific region to the west—primarily the Sierra Nevada portion—both of which have probably contributed species to the Great Basin. The factor loading with the Rocky Mountain region is the higher of the two, suggesting that the contribution from there may have been greater than that from the Sierra Nevada, as noted previously by Harper et al. (1978).

2. COLORADO PLATEAU ELEMENT.—The second factor (Fig. 4) is clearly associated with the Colorado Plateau. Its greatest representation is in the northern portion of the Colorado Plateau about the confluence of the Green and Colorado rivers. The element extends beyond the limits of the Colorado Plateau into the southeastern Great Basin. Its most abrupt attenuation occurs along the southern boundary of the Colorado Plateau in the Mogollon Rim area.

Unlike the Great Basin element, the Colorado Plateau element is not strongly correlated with any of the peripheral regions. The Colorado Plateau is also an area of relatively high endemism (Fig. 10). The high incidence of endemics and the low similarities with peripheral regions identify the Colorado Plateau element as an autochthonous element.

3. MOJAVEAN ELEMENT.—The third factor (Fig. 5) is centered about the Mojave Desert region of southeastern California, northwestern Arizona, and southern Nevada. The Mojavean element, like the Colorado Plateau element, is weakly correlated with all peripheral regions, including the Sonoran Desert region. The rapid attenuation of the element to the west, where it meets the California floristic province, is notable. The Mojave Desert region has the highest frequency of endemic species in the Southwest (Fig. 10). This element is clearly autochthonous.

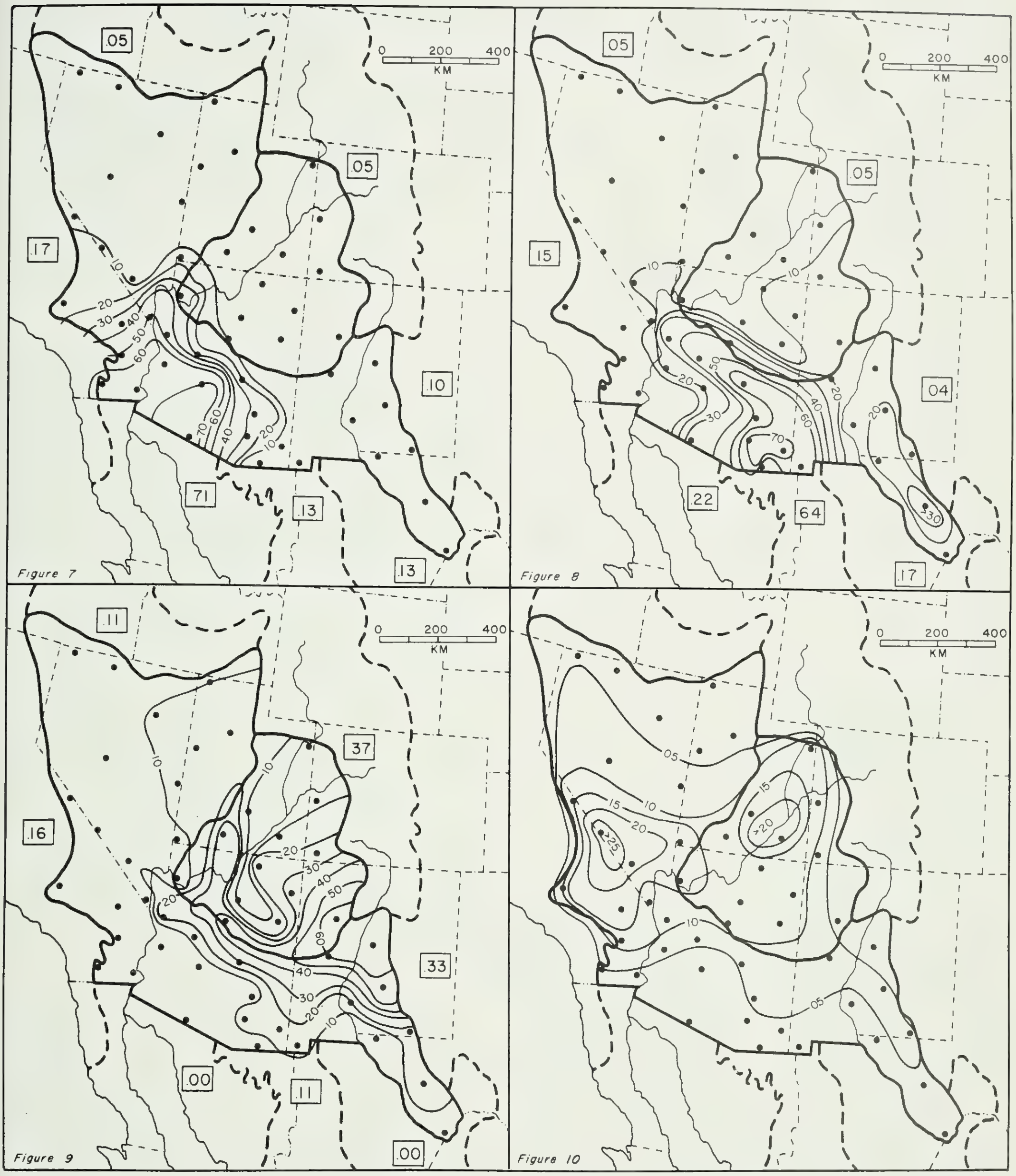
4. CHIHUAHUAN ELEMENT.—The fourth factor (Fig. 6) is identifiable as a Chihuahuan element, located in the Chihuahuan Desert area of Trans-Pecos Texas in the extreme southeastern portion of the study region. It extends up the Rio Grande Valley and into southeastern Arizona. In the latter region species with Chihuahuan affinities are frequently associated with limestone substrates (Whittaker and Niering 1968, Wentworth 1982). The Chihuahuan element is strongly correlated with the flora of the Chihuahuan peripheral region and is an extension of the flora of that region. The Chihuahuan element is also moderately correlated with the floras of the Plains and Madrean peripheral regions.

5. SONORAN ELEMENT.—The fifth factor (Fig. 7) is concentrated in southwestern Arizona and the Colorado Desert area of extreme southeastern California. It is highly correlated with the flora of the Sonoran Desert peripheral region and weakly correlated with all other peripheral regions.

The four desert elements recognized—Great Basin, Mojavean, Chihuahuan, and Sonoran—correspond very closely to the four desert regions of the same names recognized by Shreve (1942). In fact, the formal analysis presented here nicely confirms Shreve's impressions based on vegetation and flora. More recent interpretations that would include the Mojave Desert as a subdivision of the Sonoran Desert (Cronquist 1982; Turner 1982) are not supported. Floristic evidence favors retention of the Mojave Desert as a biogeographic entity distinct from the Sonoran Desert to the south.

6. APACHIAN ELEMENT. Factor 6 (Fig. 8) occurs primarily in southeastern Arizona and southwestern New Mexico. It can be termed an Apachian element in the sense of Dice (1943). The Apachian element extends all along the southern boundary of the Colorado Plateau along the Mogollon Rim into northwestern Arizona. An extension can easily be recognized in Trans-Pecos Texas and southern New Mexico east of the Rio Grande.

It is not clear from an analysis of floras from north of the International Border whether this element is largely autochthonous or allochthonous. The element could be centered within the mountainous region of southeastern Arizona, southwestern new Mexico, and northeastern Sonora, the Apachian Biotic Province of Dice (1943), or it could be a northern extension of a broader floristic element centered in the Sierra Madre Occidental of southeastern Sonora, southwestern Chihuahua, and northwestern Durango, the Sierra Madre Occidental Biotic Province of Goldman and Moore (1945). Two local floras from northwestern Mexico provide additional data. White (1948) prepared a large flora (927 native, terrestrial species) for the Rio de Bavispe region of extreme northeastern Sonora, including the Sierra del Tigre, often considered an outlying section of the Sierra Madre. Maysilles (1959) examined the flora (506 native terrestrial species) of the pine forests of western Durango in the central Sierra Madre. I have calculated the similarities between these two Mexican floras and five floras with high loadings on factor 6 (Table 7). The Bavispe flora shows high similarity with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Figs. 7–10: 7, Plot of loadings for factor 5—Sonoran floristic element. 8, Plot of loadings for factor 6—Apachian floristic element. 9, Plot of loadings for factor 7—Mogollon floristic element. 10, Distribution of species endemic to the southwestern United States. Isolines are labeled with the proportion of species in local floras occurring only in the study region.

all five floras in Table 7; the Western Durango flora shows low similarity with the same five floras. The Bavispe flora, in fact, shows significantly greater similarity with the Skull Valley flora at the western end of the Mogollon Rim region than it does with the Western Durango flora. These comparisons support an interpretation of factor 6 as an autochthonous element from the southwestern USA and northeastern Sonora. The Sierra Madre Occidental, like the Sierra Nevada and Rocky Mountains, might best be considered a floristic region separate from the Southwest region of this study. More floristic research in

TABLE 7. Comparison of selected southwestern floras with two floras from the Sierra Madre region of northwestern Mexico.

		Otsuka Similarity Index	
	Flora	Bavispe Region	Western Durango
21	Skull Valley Planning Unit	.262	.046
24	Sierra Ancha Experimental Forest	.349	.118
26	Saguaro National Monument	.459	.141
28	Chiricahua National Monument	.459	.145
29	Animas Mountains	.445	.136
	Western Durango	.172	—

northern Mexico is required to clarify relationships in this area.

7. MOGOLLON ELEMENT.—The last factor (Fig. 9) is centered in the mountainous region of central New Mexico, extending into Arizona along the Mogollon Rim, across the Kaibab Plateau, and onto the central Wasatch Plateau of southcentral Utah. This element is moderately correlated with the Rocky Mountain and Plains peripheral regions. The similarity with the Rocky Mountains region is largely due to species occurring in the southern Rocky Mountains. I have applied the designation "Mogollon" for this element because it centered about the Mogollon Rim of Arizona and the Mogollon Mountains of New Mexico.

Axelrod and Raven (1985) have recently reviewed the history of the Cordilleran Floristic Province, which they define as the Great Basin, Colorado Plateau, and Southern Rocky Mountains. They include the Mogollon area of this analysis in a Madrean Floristic Province. My analysis shows that the Mogollon area is more closely related to the Rocky Mountain region than to the Madrean region. Furthermore, the Great Basin area seems to have closer affinities with the northern Rocky Mountains than with the southern Rocky Mountains and Mogollon region. An analysis of a series of local floras situated throughout the Rocky Mountain region would be most helpful in resolving floristic relationships in the Cordilleran Region.

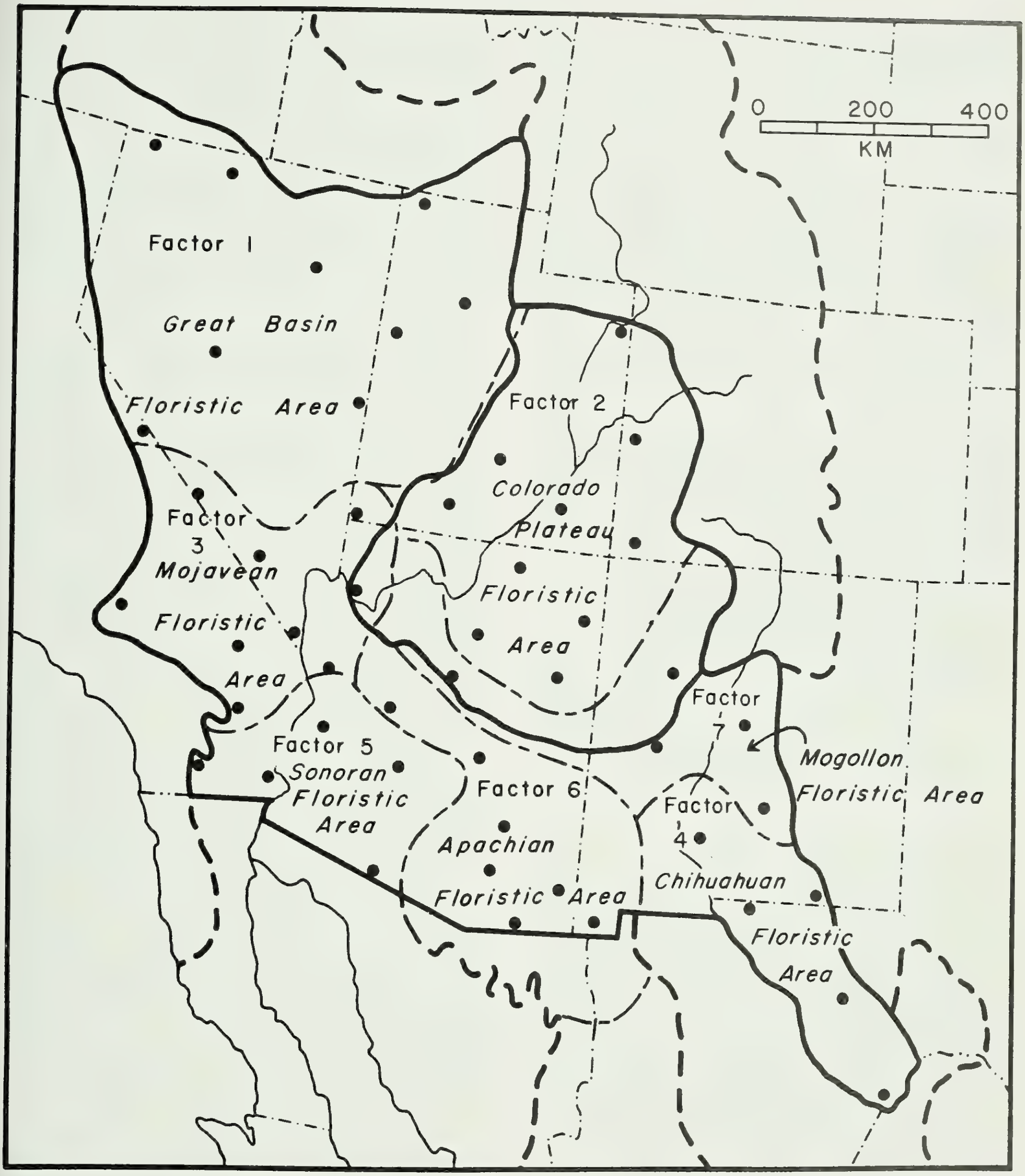
The maps of floristic elements can be combined to form a single map of floristic areas of the Southwest (Fig. 11), made simply by drawing lines around those floras sharing their highest loading with a particular factor. The position of a boundary between adjacent floras that lie in different floristic areas is determined by the relative magnitudes of the loadings between both floras and both factors. The map of floristic areas (Fig. 11) does not substitute for the maps of floristic elements. Like political units, floristic areas are two-dimensional whereas floristic elements, like representations of rainfall, temperature, or topography, are essentially three-dimensional. There is a one to one relationship between floristic elements and floristic areas in this analysis, but floristic elements are by no means confined to particular floristic areas.

The floristic areas recognized in this study are in close agreement with those of Dice (1943) for the Southwest. The only significant difference is that both my Colorado Plateau and Mogollon floristic areas would be included in Dice's Navahonian Biotic Province. The more recent treatment by Cronquist (1982) oversimplifies floristic relationships in the Southwest.

Reliability of the Analysis

Factor analysis is a nonhierarchical clustering technique that will produce clusters or factors from any data matrix. It is legitimate and important to question how accurately the factors depict the actual relationships among the variables. Does it produce the wrong clusters, or does it produce clusters when in fact none exist?

Unfortunately there are no simple statistical tests to answer these questions. I think there are two criteria that can be applied to factor analysis solutions. The first is that of interpretability. Stated simply, do the factors make sense? I have shown in the preceding section that the factors can be mapped directly to reveal their geographic meaning and that the particular factors arrived at correspond closely to floristic elements and areas in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Factor 6
Apachian
Floristic Area
Factor 7
Mogollon
Floristic Area
Factor 4
Chihuahuan
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Fig. 11. Floristic areas of the southwestern United States identified from a factor analysis of similarity coefficients among 50 local floras.

the Southwest that have been recognized for at least 40 years. The factors found in this analysis are simply and sensibly interpretable.

The second criterion is that of consistency. If relationships among the variables are weak or if there are in fact no correlated clusters of variables, small changes in the factoring procedures or in the data are likely to result in substantial changes in the final solution. To check the consistency of the factor analysis solution, I made several changes in the data analysis and compared the results. Changes included using oblique rotation instead of orthogonal rotation, substituting Simpson's index of similarity (Simpson 1960) for Otsuka's, and omitting the checklists for the seven peripheral regions from the data base. Each of the alternative analysis produced a set of seven unipolar factors nearly identical to those depicted in Figures 3–9. The factor analysis solution does appear to satisfy the criterion of consistency.

Simpson's index did appear to be superior to Otsuka's index for use in this type of analysis. The communalities, defined as the sum of the squared factor loadings for each variable, measure the proportion of variance of each variable accounted for by the final factor analysis solution. With Otsuka's index the communalities were correlated with the size of the flora ($r = 0.43$, $p < .01$); with Simpson's index the communalities and flora sizes were not correlated ($r = 0.27$, $p > .05$). This means that the unexplained or residual variances were associated with the smaller floras using Otsuka's index. Intuitively it seems more reasonable either for the residual variance to be associated with the larger floras, or for it to be uncorrelated with flora size. Also, the final solution accounts for a larger proportion of the total variance (68.7%) when the similarities are expressed as Simpson's indices.

DISCUSSION

The flora of the Southwest can be described in terms of seven floristic elements. These elements can be objectively recognized and explicitly mapped. The derived maps (Figs. 3–9) show, however, not discrete units with clearly delineated boundaries, but rather geographic features varying in intensity from a central area of greatest development and diminishing gradually outward. Each element is most clearly developed in a limited area that can be characterized by topographic and climatic features that vary from adjacent areas dominated by other elements. Five of these areas—Great Basin, Colorado Plateau, Mojave Desert, Sonoran Desert, and Chihuahuan Desert—are widely recognized natural geographic areas. The other two—Apachian floristic area and Mogollon floristic area—are readily associated with upland regions separating adjacent lowland desert areas.

Floristic elements are objectively defined assemblages, but they are not discrete, bounded units in the sense of Clementsian formations or plant association types. Each of the 50 local floras used in the analysis contains representative species of several elements; likewise the species and elemental composition of the floras change in a continuous manner along geographic gradients. The situation is analogous to weather fronts and the particular state of the atmosphere at any particular time—the existence of continuous gradients in air pressure across a region is not contradictory to the recognition of high and low pressure cells in different areas of the region.

Somewhat surprisingly the analyses failed to recognize widespread elements. That is, there were no factors that could be associated with extensive groups such as "northern," "western," "boreal," "temperate," or "southwestern" areal types (Whittaker and Niering 1964). There certainly are widespread species, i.e., those of Table 4. Such species do constitute a significant fraction of any particular *local* flora, but they constitute a small fraction of the *regional* flora. The average extent of a floristic area in this analysis includes 7 floras, but the average range of a species includes only 4 floras. In fact, only 17% of the species of the region occur in 8 or more floras, beyond the average range of one floristic area, and only 6% occur in 15 or more floras, beyond the average range of two floristic areas. In many instances one could probably associate many of the subspecific taxa of the relatively few widespread species with specific floristic elements. No widespread elements were recognized because the factors reflect general trends among the ranges of the majority of species, which are not widespread.

The recognition of floristic elements, i.e., coincident patterns in species ranges, is not necessarily inconsistent with the individualistic concept of species distributions. The latter view states that no two species distributions are identical since each species has individual physiological tolerances and evolutionary history. Indeed, very few of the over 5,000 species occurring in the Southwest show an exact correlation of presence and absence in the local floras. The existence of floristic elements indicates that species have nonrandom, overlapping patterns of area, not that they are found consistently in similar communities, which is what the individualistic concept addresses. Many southwestern species are so uncommon that they may consistently occur together in similar areas, i.e., are members of the same local floras yet seldom or never occur together in the same community.

The problem of scale or scope is thus seen to be crucial in assessing the validity of associational concepts such as elements or assemblages of species. Whittaker (1970) presents graphs of overlapping, normal curves representing the abundances of dominant, woody species in local areas to argue against the existence of vegetation association types. The quadrats or plots of the ecologist, however, contain only a minute fraction of a regional flora. As one expands the sample area from plots to local floras to floristic areas, the "grain" in species composition becomes finer and patterns emerge. At the scale of continents, I doubt that any biogeographer fails to recognize the existence of distinctive biotas.

The best explanation for groups existing at regional levels while continuity prevails at local levels involves barriers to migration. Such barriers are largely lacking for terrestrial plants at the level of quadrats and plots, but they become more common and more effective as one increases scale. At the level of continents oceans provide very effective barriers to migration; at the level of floristic areas topography and climate provide sufficiently effective barriers to promote regional differentiation of the flora into floristic elements. Important barriers in the Southwest that serve to segregate one or more floristic elements include the Mogollon Rim along the southern boundary of the Colorado Plateau, the Wasatch Plateau in central Utah, the highlands of southeastern Arizona and southwestern New Mexico (including the rather low-lying continental divide in this area), and the broad zone of increasing basal elevation in southern Nevada.

Migration has been depicted in the literature as a process that should effectively preclude the formation or recognition of floristic elements. Gleason (1926) argued that both individualistic tolerances and extensive migrations of species were inconsistent with the recognition of recurring associations of species. Good (1931) and Mason (1936) elevated to a "principle" the assertion that extensive migrations of *floras* had occurred in the past. Gleason and Cronquist (1964) stated that *most* plant species are capable of migrating to all suitable habitats and that such migrations are sufficiently rapid to keep pace with environmental changes. How then can floristic elements be maintained in the face of such extensive migrations?

The fact is that observed patterns of plant distributions in the Southwest do not provide much evidence of extensive migration as a general phenomenon. The uncommonness of the majority of species indicates either that most plants are rather poor migrators or that insufficient time has elapsed for these species to complete their migrations. Both are probably true for southwestern species.

Two observations seem to support the view that plants can and do migrate to nearly anywhere within the range of their physiological tolerances. First, many (but not all) seeds and fruits do possess obvious adaptations for dispersal. Second, the fossil record provides concrete evidence that some species have migrated widely. Nevertheless, from these observations it does not follow that all or most plant species actually have migrated extensively.

Migration is a matter of probabilities. The vast majority of seeds dispersed by plants travel very short distances (Levin and Kerster 1974). The occasional long-distance transport of a single seed or fruit is unlikely to result in successful colonization within a stable, competitive community. Most importantly, the likelihood of successful migration is dependent on the number of seeds of the species dispersed per unit of time compared to other potential migrators. The majority of plant species in the Southwest occur in three or fewer local floras and may simply not be abundant enough to generate a flux of seed sufficiently great to make extensive migration likely, even over considerable spans of time.

Most of the actual examples of extensive migration in the fossil record involve dominant, usually woody species. These plants constitute a small fraction of the southwestern regional flora. Derivation of general principles for all species of plants from data on the current and former distributions of species such as redwoods, sugar maples, and other forest trees is a questionable practice that may have led to some unwarranted conclusions.

If the capacity of most species to migrate to all areas suited to their physiological tolerances were as pervasive as typically assumed, I would expect the average range of a species to be much wider. One could argue that species in the Southwest have very narrow physiological tolerances that effectively restrict them to relatively few habitats within a limited area, but that seems rather unlikely given the similar nutritional needs of plants and the apparent lack of coincidence between most species and very specific habitats. It seems much more likely that barriers to migration, competition, and low rates of seed dispersal interact to greatly curtail the ability of most species to migrate.

Over the past several years a general model of southwestern phytogeographic history has emerged that includes several postulates: (1) most species present today had evolved by the end of the Tertiary, (2) these species have undergone extensive and intensive migrations in response to Pleistocene climate changes, and (3) modern plant distributions reflect both this migrational history and the tolerances of species for modern climatic conditions.

The concept of great species longevity is supported by Levin and Wilson (1976), who estimated the mean duration for herbaceous species to be 10 million years, with a mean speciation rate of 1.15 lineages per million years. Woody species were estimated to be even more persistent and to have even slower rates of speciation. Consistent with this view, Tidwell et al. (1972) hypothesized that the flora at the beginning of the Pleistocene in the Intermountain Region was basically the same as exists today.

The best evidence that many dominant species have indeed undergone extensive migrations in the Southwest at the end of the Pleistocene comes from fossil packrat middens (Van Devender and Spaulding 1979, Wells 1983). Many workers have textraploted these results back to previous glacials and interglacials, concluding that the repeated climate changes occurring during the Pleistocene in topographically heterogeneous intermountain environments would have kept species populations in constant movement (Cronquist 1978).

It is difficult to conceive how recognizable floristic assemblages could survive through the Pleistocene with all this movement, fluctuation, and shuffling of populations in response to climate change. My analysis of modern plant distributions in the entire regional flora, however, casts some doubt on the generality of the consensus model outlined above. Most of the local floras included in this analysis are from areas encompassing extensive elevational relief. Southwestern mountain ranges, particularly in the Basin and Range Province, possess considerable habitat diversity in association with elevation, typically going from desert at the base to pinyon-juniper woodland, pine forest, or even spruce forest at the top (e.g., Lowe 1964). Old species with extensive migrational histories would have left relictual populations scattered within and between these ranges. Only a single, small population is required to establish a species as a member of a local flora. The consensus model would predict that the ranges of most species would include many such scattered, relictual populations, resulting in a modern flora with most species widely distributed throughout the region and little differentiation of the floristic assemblages within the region.

Many species, particularly those of high elevations, do show distribution patterns consistent with the consensus model, but they do not constitute a large fraction of the Southwest flora. For the rare species consisting of small populations in only a few floras, i.e., the majority of species in the Southwest today, extinction, rather than migration, is the more likely response to severe climate change. These species are unlikely to possess sufficient ecotypic, genetic diversity or sufficiently large populations required to keep pace with the changing environment.

Speciation, however, may also be accelerated during periods of severe climate change (Stebbins 1947, Axelrod 1981). Many southwestern species probably originated in postglacial time in response to the new, more arid environments created by the changes from Pleistocene to Holocene climates. Such an interpretation has been applied to *Atriplex* (Stutz 1978) and seems likely for many of the species of large southwestern genera such as *Eriogonum, Astragalus, Penstemon, Gilia, Camissonia, Cryptantha, Phacelia, Opuntia,* and others.

Do we need two models of evolutionary response to climate change, one for common species and one for rare species? I think not. Common plant species consist of many populations of subspecies, varieties, or ecotypes. During periods of severe climate change, some of these ecotypes will migrate, many will go extinct, and some will differentiate to form new ecotypes, varieties, subspecies, and species in new habitats. As a result, the range of the species before the climate change (i.e., in the fossil record) will be different from its range after the climate change. But migration of populations or ecotypes existing before the climate change and persisting through the climate change need account for only part of the total change in the range of a species. In other words, the most likely response of any particular small population to rapid environmental change is extinction; the probability of a species becoming extinct depends in large part on how many populations it has.

The seven floristic elements identified in the present analysis are clearly associated with modern, Holocene environments. They represent centers of postglacial differentiation and speciation within the depleted flora surviving at the end of the Pleistocene in the Southwest, partially but effectively isolated from adjacent elements by modern climatic and topographic barriers.

My analysis of specific similarities among local floras of the Southwest is consistent with a hypothesis of Holocene differentiation of the modern regional flora. An analysis of generic similarities among these floras might better reflect the Tertiary and Pleistocene migrational history of the flora, since the majority of the genera are doubtless of Tertiary age. My interpretation of the evolution of the southwestern flora is also consistent with the concept of punctuated equilibria, as opposed to slow, gradual phylogenetic change, which would be more consistent with the consensus model discussed above.

American plant ecology has been very much a science of dominants. This bias has been carried over into plant geography, which has emphasized the distribution of vegetation almost to the exclusion of flora. I have tried to show in this paper how a study of the entire flora of a region, weighing all species equally, can reveal patterns that may not follow from or be in agreement with principles and models derived solely from study of the dominant species. Floristics and vegetation analysis are complementary approaches to understanding the distribution and abundance of plants. Phytogeography needs both.

Acknowledgments

I thank R. M. Turner, J. H. Brown, J. E. Bowers, and M. A. Kurzius for reading and commenting on the manuscript. M. Beauchamp, J. E. Bowers, D. Clemons, R. A. Fletcher, T. R. Van Devender, and R. D. Worthington helped in the acquisition of floras and unpublished checklists. The illustrations were prepared by M. A. Kurzius.

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UTAH FLORA: APIACEAE (UMBELLIFERAE)

Sherel Goodrich[1]

ABSTRACT.—Eighty-four taxa in 30 genera of the parsley family, Apiaceae (Umbelliferae) are treated for Utah. Four of the genera with one species each that escape from cultivation are included in the key but not in the text. Keys to genera, species and infraspecific taxa are provided, along with detailed descriptions, distributional data, and pertinent comments. Proposed new taxa are *Cymopterus acaulis* (Pursh) Raf. var. *parvus* Goodrich and *Lomatium scabrum* (Coult. & Rose) Mathias var. *tripinnatus* Goodrich. New combinations include: *Cymopterus acaulis* (Pursh) Raf. var. *fendleri* (Gray) Goodrich and var. *higginsii* (Welsh) Goodrich; *Cymopterus purpureus* Wats. var. *jonesii* (Coult. & Rose) Goodrich and var. *rosei* (Jones) Goodrich; *Cymopterus terebinthinus* (Hook.) T. & G. var. *petraeus* (Jones) Goodrich.

This paper is another in a series leading to a definitive treatment of the flora of Utah. Previous papers have dealt with the Brassicaceae (Cruciferae), Fabaceae (Leguminosae), Rosaceae, Asteraceae (Compositae), Salicaceae, Cactaceae, Chenopodiaceae, and miscellaneous smaller families.

The parsley family presents a formidable challenge to students of plant taxonomy and to others who need to identify its members. The family itself is well marked, but some generic lines within it are fraught with difficulty. It is interwoven with look-alikes often of different and sometimes distantly related genera. Floral structures are reduced and uniform. The calyx is lacking or reduced to mere teeth. Petals are only about 1–2 mm long in our taxa except in *Heracleum*. Color variation of petals is basically restricted to yellow and white, and occasionally purple. Yellow petals very often turn white or cream when dried, and a number of taxa described from dried specimens as having white petals have been proven by field studies to have fresh petals that are yellow. The reduction and uniformity of floral parts requires the use of fruiting and vegetative features for separation of taxa. The features of the mature fruit are quite diagnostic, but this does not help in identification of specimens collected in flowering condition. Vegetative features are used extensively in the keys of this work, but these features are extremely variable. The size of the family (30 genera and 84 taxa in Utah and about 300 genera and about 3,000 species worldwide) also contributes to difficulty in identification.

Among those of the Old World introduced, cultivated members of the family are caraway (*Carum carvi*), carrot (*Daucus carota* ssp. *sativus*), celery (*Apium graveolens*), dill (*Anethum graveolens*), ground elder (*Aegopodium podagraria*, parsley (*Petroselinum crispum*), and parsnip (*Pastinaca sativa* ssp. *sylvestris*). Other introductions from the Old World include: hedge parsley (*Torilis arvensis*), poison hemlock (*Conium maculatum*), sweet fennel (*Foeniculum vulgare*), wild carrot (*Daucus carota* ssp. *carota*), and wild parsnip (*Pastinaca sativa* ssp. *sativa*). The toxic nature of poison hemlock has long been known, and water hemlock (*Cicuta maculata*) is probably the most violently poisonous plant of our native flora. Many other members of the family such as western sweet cicely (*Osmorhiza occidentalis*) and spring parsley (*Cymopterus* spp.) are used extensively by livestock and wildlife without apparent harm.

Measurements of rays, pedicels, and fruit were taken from specimens with mature fruits. At the end of the discussion of each taxon there are two numbers. The first, in Arabic numerals, indicates the number of Utah specimens examined for the taxon. The second, in Roman numerals, indicates the number collected in Utah by the author.

ACKNOWLEDGMENTS

Appreciation is expressed to Dr. Arthur Cronquist for permitting me to examine his

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Apiaceae manuscript for the Intermountain Flora. His observations of the carpophore in *Cymopterus* have been especially helpful. Beverly Albee helped with distribution maps for all species. These maps were helpful to understanding possible relationships of taxa as well as distributions. Appreciation is also expressed to the directors and curators of the following herbaria of the state: Brigham Young University, Provo; Forest Service Herbarium, Ogden; Garrett Herbarium, The University of Utah, Salt Lake City; Intermountain Herbarium, Utah State University, Logan. I appreciate the loans from each of these herbaria. These specimens are the basis of this work. During the course of this project, numerous specimens have been sent to Dr. Lincoln Constance (a student of the family for more than 40 years) for annotation. His prompt and congenial replies are greatly appreciated. The concepts of several taxa are based on his annotations. This work is dedicated to him.

APIACEAE (UMBELLIFERAE)

Parsley Family

Annual, biennial, or perennial acaulescent or caulescent herbaceous plants from taproots, rhizomes, fibrous or tuberous roots, or caudices; leaves simple to decompound, petioles often dilated and partly sheathing at the base or the upper leaves reduced to dilated sheaths; inflorescence mostly of compound umbels, the primary umbels with or without a subtending involucre of bracts, the secondary umbels (umbellets) with or without a subtending involucel of bractlets; flowers mostly regular, perfect, or some of them staminate or sterile; calyx of 5 teeth or lobes, or obsolete, or lacking; petals 5, small, usually inflexed at the tip, mostly white or yellow, occasionally purple; stamens 5, small, alternate with the petals; ovary inferior, bicarpellate, 2-loculed, with 1 ovule per locule, the two styles with or without a conical base (stylopodium); fruit a dry schizocarp of 2 mericarps united by their faces (the commmissure) nearly terete, dorsally compressed (compression parallel to a broad commissure), or laterally compressed (compression, contrary to a narrow commissure); mericarps separating at maturity and apically attached to and pendulous from a fine wirelike entire or bifid to divided carpophore or remaining adherent and then the carpophore usually lacking or poorly developed and usually adnate to the commissural faces, each mericarp usually 5-nerved, 3 of the nerves dorsal and 2 on the lateral margins, the nerves filiform to winged, or obscure or lacking, the intervals between the nerves commonly with 1 or more oil-tubes, the commissural faces often with 2 or more oil-tubes.

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MATHIAS, M. E., AND L. CONSTANCE. 1944–1945. Umbelliferae. N. Am. Fl. 28B:43–297.

1. Leaves peltate, simple, orbicular; flowers in a verticellate spikelike inflorescence; plants rhizomatous, of Washington County . . . . *Hydrocotyle*

— Leaves not as above; flowers in compound umbels, or globose heads (in a few taxa of *Cymopterus*); plants rarely rhizomatous 2

2(1). Plants caulescent; pseudoscape lacking; the few to several peduncles mostly shorter than the leafy stem on which they are borne; styles rarely over 1 mm long; stylopodium present and petals white in native taxa except *Zizia* and in a few taxa keyed both ways 3

— Plants acaulescent, the leaves sometimes whorled atop a pseudoscape, or if subcaulescent then the usually solitary peduncle longer than the short, leafy stem on which it is borne, and lateral umbels if any mostly borne on the lower 1/3 of the plant; styles often over 1 mm long; stylopodium lacking in all but *Podisteria* and in taxa keyed both ways; petals yellow, white, or purple 4

3(2). Leaves simple, pinnate or ternate; leaflets mostly sessile. . . . . Key I

— Primary leaflets usually petiolulate . . . . . Key II

4(2). Leaves ternate or biternate with 3–9 leaflets or rarely a few simple, usually only 2–3 per plant; leaflets 1.5–7 (11.5) cm long, entire, linear or nearly so; plants 5–10 cm tall, from a globose or fusiform tuber; petals white . . . . *Orogenia*

— Leaves and leaflets not as above or if so then plants mostly taller and/or petals yellow 5

5(4). Stylopodium low conic; plants of the Raft River and Uinta mountains, mostly above 2,440 m, sometimes with a lateral umbel in the axil of a bract or leaf on the upper 1/2 of the stem, glabrous; involucels lacking or of 1–2 linear bractlets; fruit 3–6 mm long; petals white . . . . *Ligusticum*

— Stylopodium lacking except in *Podistera*; plants not as above in all features; involucels mostly present; fruit mostly longer or petals yellow 6

6(5). Key to plants with mature fruits . . . . Key III

— Key to plants in flower or with young fruits . . . . Alternate Key III

Key I

Plants caulescent; the few to several peduncles and umbels mostly shorter than the leafy stem; stylopodium present in all but *Zizia* and two other taxa that are keyed both ways; leaves simple, pinnate, or ternate; leaflets sessile.

1. Leaflets entire, linear or linear-elliptic 2

— Leaflets toothed and/or lobed, not linear 4

2(1). Leaves soon withering, some usually deciduous shortly after anthesis, some leaflets often more than 1.5 cm long; plants from a tubrous root or fascicle of tuberous roots, the stem readily detached from the tubrous base, from northern Utah; stylopodium present . . . . *Perideridia*

— Leaves more persistent, the leaflets not more than 1.5 cm long or plants of San Juan and Wayne counties; plants from a taproot with a branched crown or caudex; stylopodium lacking 3

3(2). Petals and stamens yellow when fresh; leaflets mostly 2–5 cm long; fruit 6–8 mm long; plants of San Juan and Wayne counties . . . . *Cymopterus beckii*

— Petals and stamens white; leaflets 0.3–2 cm long; fruit 2–4 mm long; plants of Cache County . . . . *Musineon lineare*

4(1). Basal leaves mostly simple, shallowly toothed, cordate at the base; stem leaves usually ternate, not over 3 cm long; petals bright yellow . . . . *Zizia*

— Leaves pinnate, or if ternate or upper ones simple then over 3 cm long; petals white or yellow 5

5(4). Leaves ternate, the upper ones sometimes simple, the 3 leaflets 8–36 cm long, about as wide; plants 1–2 m tall or taller, villous-woolly at least on some of the nodes; the larger petals 4–8.5 mm long . . . . *Heracleum*

— Leaves pinnate, the leaflets less than 8 cm long and much narrower; plants shorter or not villous-woolly; petals smaller 6

6(5). Umbels sessile or nearly so; leaflets ovate to suborbicular, 3-lobed to near the middle; fruit about 1.5 mm long; plants cultivated and rarely escaping except in Washington County (celery) . . . . *Apium graveolens* L.

— Umbels not sessile except sometimes the terminal one; leaflets variously shaped, but not ovate to suborbicular and lobed to near the middle; fruit more than 1.5 mm long except in *Berula*, plants various 7

7(6). Involucre and involucels well developed, sometimes spreading or deflexed, the bracts 1–6, the bractlets (2) 4–12; fruit 1.5–3 mm long, the ribs not winged; plants of very wet places, often growing in water, from fibrous roots 8

— Involucre lacking or infrequently of 1 or 2 bracts; involucels often lacking; fruit over 3 mm long or else the ribs winged; plants of various habitats, from a taproot or tuberous roots 9

8(7). Stems often sprawling, sometimes stoloniferous; leaves with (3) 5–15 opposite pairs of leaflets, these 0.3–4 (6.5) cm long; rays 4–16; ribs of the fruit obscur . . . . *Berula*

— Stems erect, not stoloniferous; leaves with 4–6 opposite pairs of leaflets, these 2–8 (15) cm long; rays 11–24; ribs of the fruit prominently corky . . . . *Sium*

9(7). Umbels often more than 7 per stem; fruit strongly flattened dorsally, 5–8 mm long, 3–6 mm wide, the lateral ribs slightly winged, the dorsal ones filiform; petals greenish yellow or reddish; plants introduced, cultivated and wild . . . . *Pastinaca*

— Umbels mostly less than 7 per stem; fruit not strongly flattened dorsally or if so only 3–5 mm long; petals white or greenish; plants native 10

10(9). Fruit over 1 cm long; leaves rarely all pinnate; peduncles mostly not subtended by dilated, bladeless sheaths or these greatly reduced . . . . *Osmorhia*

— Fruit 3–5 mm long, leaves mostly all once pinnate; peduncles often with subtending dilated sheaths 11

11(10). Fruit strongly flattened, the dorsal ribs filiform, the lateral ribs conspicuously winged; plants from fascicles of tuberous roots, of the Abajo and La Sal mountains . . . . *Oxypolis*

— Fruit rounded in cross section, the dorsal and lateral ribs with small wings; plants from a taproot, widespread . . . . *Angelica*

Key II

Plants caulescent; the few to several peduncles and umbels mostly shorter than the leafy stems; stylopodium present or plants also keyed in Key III; leaves more than once-compound; primary leaflets not sessile.

1. At least some of the ultimate leaf segments over 2 cm long, toothed or lobed, but not entire or pinnatifid 2

— Ultimate leaf segments less than 2 cm long or if longer then entire or pinnatifid 5

2(1). Plants from creeping rhizomes, cultivated and rarely escaping; lower leaves long-petioled, often biternate with 9 leaflets but sometimes irregularly compound (ground elder) . . . . . . *Aegopodium podagraria* L.

— Plants not from creeping rhizomes, seldom cultivated; leaves various 3

3(2). Involucels of about 6 bractlets, 1–4 mm long; umbels 6–20 or more per stem, the rays 15–26, 1.5–4 cm long; fruit 2–4 mm long, the ribs corky . . . . . . *Cicuta*

— Involucels mostly lacking; umbels often fewer than 6 per stem and/or the rays either fewer or longer than above or both; fruit 4–25 mm long, the ribs various 4

4(3). Fruit (10) 12–25 mm long, bristly pubescent in 2 of 3 species, the dorsal ribs not prominent; leaflets often hirtellous; dilated sheaths seldom subtending the peduncles . . *Osmorhiza*

— Fruit 4–5 mm long, not bristly pubescent, the dorsal ribs with small wings; leaflets glabrous; peduncles often subtended by dilated bladeless (or nearly so) sheaths . . . . . . *Angelica*

5(1). Fruits and ovaries with bristly hairs; involucre often of pinnatifid or compound bracts; plants annual or biennial 6

— Fruits and ovaries without bristly hairs; involucre mostly of entire bracts; plants mostly biennial or perennial 8

6(5). Involucre lacking or of 1 entire bract; plants with appressed hispid hairs, from Washington County . . . . . . *Torilis*

— Involucre of few to several pinnatifid to compound bracts; plants glabrous or with spreading hairs 7

7(6). Bracts of the involucre leaflike, pinnately compound; rays 1–7 (9), 1.5–10 cm long, some much longer than the involucres, some often nearly as long as the peduncles; inflorescence open; bristly hairs of the fruit hooked; plants annual, of Washington County . . . . . . *Yabea*

— Bracts of the involucre pinnatifid; rays mostly 10–60 or more, seldom over 3 cm long or if longer then plants biennial, often not much exceeding the involucres, rarely longer than the peduncles; inflorescence congested; bristly hairs of the fruit glochidiate at apex; plants widespread . . . . . . *Daucus*

8(5). Involucel and involucre lacking 9

— Involucel and sometimes involucre present . . 13

9(8). Petals yellow; plants introduced, cultivated and adventive, ultimate segments of leaves filiform, 0.1–4 cm long, about 0.5 mm wide 10

— Petals white, or yellow in *Lomatium* and then plants native; ultimate segments various but often over 0.5 mm wide 11

10(9). Plants annual, not glaucous, widely cultivated; leaves not especially crowded toward the base of the plant, the petiolules of the lowest pair of primary leaflets mostly less than 2 cm long, the ultimate segments 4–20 mm long (dill) . . . . . . *Anethum graveolens* L.

— Plants perennial, glaucous, occasionally adventive; leaves sometimes crowded toward the base of the stem, the petiolules of the lowest pair of primary leaflets often over 2 cm long, the ultimate segments 4–40 mm long . . . . . . *Foeniculum*

11(9). Plants biennial from taproots, introduced; umbels often 6–12, or more per stem; fruit 3–4 mm long, the ribs filiform, not at all winged . . . . . . *Carum*

— Plants perennial from taproots or caudices, native; umbels rarely more than 8 per stem; fruit 3–14 mm long, the lateral and sometimes the dorsal ribs winged 12

12(11). Petals white; fruit 3–8 mm long, rounded, the dorsal and lateral ribs narrowly winged; stylopodium low conic; ultimate leaflets over 50 per leaf, 0.1–1 (1.5) cm long . . . . . . *Ligusticum*

— Petals yellow when fresh; fruit 8–14 mm long, dorsally flattened, the dorsal ribs filiform, the lateral ribs winged; stylopodium lacking; ultimate leaflets usually 3–45 per leaf, 0.3–9 cm long . . . . . . *Lomatium*

13(8). Petals yellow or greenish yellow; plants cultivated, rarely escaping (Parsley) . . . . . . *Petroselinum crispum* (Mill.) A. W. Hill

— Petals white; plants not cultivated 14

14(13). Stems often purple-spotted, usually much branched, mostly with 10–30 or more umbels; plants 5–30 dm tall, naturalized, weedy in moist or wet places in valleys and foothills, occasionally montane; involucre of 2–6 bracts, 2–6 (15) mm long . . . . . . *Conium*

— Stems not purple-spotted with few branches, with (1) 3–7 (12) umbels; plants to 10 dm tall, native, often montane, involucre lacking or seldom as above 15

15(14). At least some of the ultimate leaflets 2–6 cm long and entire; leaves often withering shortly after anthesis; plants from a tuberous root or fascicle of tuberous roots, these easily detached from the stem, and often missing in herbarium specimens . . . . . . *Perideridia*

— Ultimate leaflets not over 2 cm long or if so not entire; leaves more persistent than above; plants from a taproot or a cluster of fleshy-fibrous roots 16

16(15). Involucels usually with more than 3 bractlets; fruit slightly compressed dorsally; root-crown mostly simple, without old long-persisting petiole-bases; plants rather rare in the eastern half of the state . . . . . . *Conioselinum*

— Involucels lacking or rarely with more than 3 bractlets; fruit terete or slightly compressed laterally; root-crown simple or branched, usually with fibrous long-persisting petiole-bases; plants common, widespread . *Ligusticum*

Key III

Plants acaulescent, sometimes with a pseudoscape, or if subcaulescent then the mostly solitary peduncle longer than the short, leafy stem on which it is borne and lateral umbels if any mostly borne on the lower 1/3 of the plant; styles often over 1 mm long; stylopodium mostly lacking.

1. Fruit strongly flattened dorsally, the dorsal ribs filiform, not winged, the lateral ribs more or less winged, the body 8–15 (20) mm long or if shorter then plants usually pubescent (note: *L. cous*, *L. minimum*, and *L. scabrum* have small fruits and glabrous herbage); involucre lacking .... *Lomatium*

— Fruit not strongly flattened or if so the dorsal ribs winged, the body usually less than 8 mm long, the wings sometimes to 12 (15) mm long especially in plants with an involucre; plants glabrous to hirtellous 2

2(1). Stylopodium conic; leaves once compound with palmatifid leaflets; bractlets of involucels with 2–3 or more teeth; plants known from high elevations of the La Sal Mountains where apparently rare .... *Podistera*

— Stylopodium lacking; leaves either more than once compound or leaflets not palmatifid; bractlets entire or plants not of high elevations of the La Sal Mountains (except *Oreoxis bakeri*) 3

3(2). Ribs of fruit not winged or at most with low corky wings; carpophore well developed; leaves pinnate, a few of the leaflets sometimes pinnatifid and nearly bipinnate; plants of Cache, Garfield, and San Juan counties 4

— Ribs of the fruit with papery wings or if with low, corky wings then the carpophore lacking; leaves usually more than once compound; plants of broad distribution 5

4(3). Ribs of fruit not winged; terminal umbel often subtended by a smaller umbel; petals and stamens white; plants often subcaulescent, of the Bear River Range, Cache County .... *Musineon*

— Ribs of fruit with low, corky wings; umbel solitary; petals and stamens yellow; plants strictly acaulescent, of Garfield and San Juan counties (note: our plants may not have a carpophore) .... *Aletes*

5(3). Fruit slightly compressed laterally, with low corky wings, 2–5 mm long and with rather conspicuous, persisting calyx teeth, the carpophore lacking; plants from branched caudices, strictly acaulescent, not strongly aromatic, mostly hirtellous or scabrous throughout or else the bractlets toothed, 1–10 (15) cm tall, montane, mostly above 2,440 m except in *O. trotteri*................. *Oreoxis*

— Fruit compressed dorsally with prominent, more or less papery or corky wings, the calyx teeth obsolete or not persisting or else the carpophore well developed; plants from fibrous often enlarged tuberlike taproots, or if from branched caudices then with one or more of the following features: with one or more cauline leaves and from lower elevations, strongly aromatic, glabrous, regularly over 10 cm tall; bractlets often not toothed .... *Cymopterus*

Alternate Key III

Plants with features of Key III but in flower or with immature fruits.

1. Leaves pinnate or pinnatifid, rarely trifid with linear entire segments 2

— Leaves either more than once-compound or else ternate or ternately divided with toothed to lobed leaflets 7

2(1). Petals and stamens white; terminal umbel sometimes subtended by a smaller axillary umbel; plants of Cache County ..... *Musineon*

— Petals and stamens yellow when fresh; umbel solitary; plants of the southern 1/2 of the state 3

3(2). Bractlets of the involucel usually with 3 or more teeth or lobes linear-elliptic or oval to obovate; stylopodium present or lacking; plants of the La Sal Mountains 4

— Bractlets of the involucel mostly entire, linear or narrowly elliptic; stylopodium lacking; plants not known from the La Sal Mountains 5

4(3). Leaflets more or less palmatifid, the major segments again trilobate to palmatifid; stylopodium conspicuous; base of plant with few if any persisting leaf bases .... *Podistera*

— Leaflets pinnatifid or trifid; stylopodium lacking; base of plant clothed with persisting leaf bases .... *Oreoxis bakeri*

5(3). Leaflets entire, 0.5–2 mm wide, linear-filiform to very narrowly elliptic; plants of Emery, Garfield, Iron, Sevier, and Wayne counties......................... *Lomatium*

— At least some of the leaflets lobed, or if all entire then some over 2 mm wide and elliptic; distribution various 6

6(5). Leaflets 0.3–1.2 cm long; rays 4–8, 2–10 mm long; involucels 4–5 mm long; plants of Garfield and central San Juan counties . . *Aletes*

— Some of the leaflets regularly over 1.2 cm long; rays (4) 6–13, 5–20 mm long; involucels 2–15 mm long; plants of Grand and extreme northern San Juan counties . *Lomatium latilobum*

7(1). Plants pubescent, not more so just below the umbel than elsewhere (see also *Oreoxis alpina*) . . . . *Lomatium*

— Plants glabrous or scabrous, sometimes hirtellous just below the umbel and then with glabrous leaves 8

8(7). At least some of the ultimate leaflets over 2 cm long and entire or at most toothed 9

— Ultimate leaflets less than 2 cm long or if longer then lobed 10

9(8). Peduncles hirtellous just below the umbel, glabrous below; leaves glabrous, lowest pair of primary leaflets sessile or on petiolules less than 2 cm long, the ultimate leaflets to 2.5 cm long, 1–3 (4) mm wide; plants not aromatic, from the southern 1/2 of the state . . . . *Cymopterus lemmonii*

— Plants glabrous or if scabrous then not more so just below the umbel than elsewhere; lowest pair of primary leaflets either with petiolules longer than above or some of the ultimate leaflets mostly longer or wider than above; plants of the northern 1/2 of the state or else strongly aromatic . . . . *Lomatium*

10(8). Plants from a taproot, this sometimes enlarged and tuberlike, the crown simple or few-branched, with few if any long-persisting leaf bases; pseudoscape (at least a subterranean one) often conspicuous; leaf blades sometimes with confluent portions that are wider than the ultimate teeth or lobes 11

— Plants from a simple or more often branched often woody caudex, this often clothed with long-persisting leaf bases; pseudoscape lacking; leaf blades finely and completely dissected so that the ultimate segments are the widest undivided portions of the blade 12

11(10). Taproot very slender, with 1 or more abruptly expanded globose or ovoid tuberlike segments; plants strongly aromatic and from Salt Lake County north to Cache County or if not aromatic then of northwestern Box Elder County (*L. ambiguum* and *L. cous*) . . *Lomatium*

— Taproot slender or enlarged, if with a tuberlike enlargement then this gradually expanded from a narrow portion; plants not aromatic, distribution various (note: rare glabrous specimens of *Lomatium junipernum* will key here) . . . . *Cymopterus*

12(10). Leaves with only about 2–4 opposite pairs of primary leaflets; plants of mountains, mildly if at all aromatic 13

— At least some of the leaves with 5–11 opposite pairs of primary leaflets; plants of mountains and deserts, aromatic or not 14

13(12). Primary leaflets 4–14 mm long, sessile; leaf blades 1–3.5 cm long; plants to about 12 cm tall, scabrous-hirtellous throughout or else bractlets of the involucel toothed . . . . . . *Oreoxis*

— At least the lowest pair of primary leaflets usually 15–35 mm long, sessile or on petiolules to 15 mm long; plants 8–50 cm tall, glabrous except hirtellous on the peduncle just below the umbel and sometimes scabrous or hirtellous in the umbel, bractlets of the involucel entire . . . . *Cymopterus lemmonii*

14(12). Lowest pair of primary leaflets seldom over 1/4 as long as the leaf blade, sessile or on petiolules to 18 mm long; leaves pinnately compound, the blades more or less oblong in outline 15

— Lowest pair of primary leaflets (1/4) 1/3–3/4 as long as the leaf blade, on petiolules over 18 mm long; leaves more or less ternate-pinnately compound, the blades often ovate in outline 16

15(14). Segments of leaves 1–12 mm long; some bractlets of the involucels usually exceeding the flowers; plants widespread, mostly of high elevations . . . . *Cymopterus hendersonii*

— Plants growing 792–2,320 m, or if of higher elevations then scabrous and ultimate segments of leaves 1–4 mm long; bractlets of the involucel rarely exceeding the flowers; plants of the southern 1/2 of the state, mostly of low to moderate elevations (*L. parryi* and *L. scabrum*) . . . . *Lomatium*

16(14). Calyx teeth lacking or to 0.3 mm long; ultimate segments of leaves 0.2–0.3 mm wide . . . . *Lomatium grayi*

— Calyx teeth 0.5–0.9 mm long; ultimate segments of leaves 0.5–1 (1.5) mm wide . . . . *Cymopterus terebinthus*

Aletes Coult. & Rose

Perennial, acaulescent, glabrous to pubescent herbs; leaves pinnate or bipinnate, petiolate, the leaflets distinct or confluent, often lobed and spinulose-dentate or entire; umbels compound; involucre lacking; rays few to several, spreading to reflexed; involucel of free or united bractlets; calyx teeth conspicuous, deltoid-ovate; stylopodium lacking; carpophore divided to the base, sometimes readily deciduous; fruit oblong to ovoid-oblong, slightly compressed laterally or subterete, the ribs subequal, prominently corky-winged or obscure.

***Aletes macdougalii* Coult. & Rose** Plants 7–20 cm tall, acaulescent, glabrous or scabrous, from a branched caudex, this more or less clothed with persistent leaf bases; leaves pinnate or some of the leaflets pinnatifid and nearly bipinnate, with 2–6 opposite pairs of lateral leaflets or lobes, petioles 1.5–7 cm long, blades 1–5 cm long; leaflets 0.3–1.2 cm long, sessile, narrowly elliptic and entire or obovate and with 1–3(5) teeth or lobes; peduncles 5–15 cm long; umbel solitary; rays 4–8, 0.2–1 cm long; bractlets of the involucel about 4–6, 4–5 mm long, linear or linear-elliptic, more or less united at the base; pedicels 1–2 mm long; calyx teeth about 1–1.5 mm long, narrowly to broadly deltoid; petals yellow when fresh; styles 1.5–2.5 mm long; fruit 4–6 mm long, the ribs with small, more or less corky wings, the lateral ones about 1 mm wide, the dorsal ones smaller. Rock crevices, rocky slopes, and sandy ground, in pinyon-juniper and limber pine-bristlecone pine communities at 1,280 to 2,740 m in Garfield and San Juan counties; Arizona, Colorado, and Utah; 8(0). Our plants are referable to ssp. *breviradiatus* Theobald & Tseng. They could reasonably be included in the genus *Cymopterus*.

Angelica L.

Perennial, caulescent, single-stemmed herbs from a stout taproot; leaves pinnately to ternately 1–3 times compound, with broad leaflets; the lower blades on elongate petioles, the middle ones often arising directly from a dilated sheath, the upper ones often much reduced or lacking and the leaves reduced to a dilated sheath; umbels compound; involucre and involucel lacking or of narrow scarious or foliaceous bracts or bractlets; calyx teeth minute or obsolete; petals white, seldom pink or yellow; stylopodium broadly conic; carpophore divided to the base; fruit elliptic-oblong to orbicular strongly compressed dorsally, the lateral and dorsal ribs with small but obvious wings, or the ribs sometimes all corky-thickened and scarcely winged.

1. Leaflets mostly lanceolate to nearly linear, mostly over 3 times as long as wide; leaf blades oblong in outline; umbels 2–7, with 7–20 rays 2

— Leaflets ovate or broader, or if lanceolate and over 3 times as long as wide then umbels mostly more than 7, and rays 20–40 3

2(1). Leaves ternate-pinnate, the lowest pair of primary leaflets on petiolules 3.5–12 cm long; leaflets coarsely toothed to lobed, the margins with about 1–3 teeth or lobes per cm; plants of the Deep Creek Mountains . . . . *A. kingii*

— Leaves pinnate or scarcely ternate-pinnate, the lowest pair of primary leaflets sessile or on petiolules to 1.5 cm long; leaflets finely to rather coarsely toothed, the margins with about 3–7 teeth per cm; plants not known from the Deep Creek Mountains . . . *A. pinnata*

3(1). Plants not over 1 m tall, mostly of rocky places above 3,050 m; umbels 1–3; leaflets 1–5 cm long, serrate-dentate, rarely lobed; involucels of 1–3 or more linear bractlets about 3–10 mm long; ovaries and fruit glabrous or at most scabrous . . . . *A. roseana*

— Plants mostly 1–2 m tall, mostly of wet places below 3,050 m; umbels several; leaflets 3–16 cm long, some usually lobed as well as toothed; involucels lacking; ovaries and young fruit hispid to hirsute . . . . *A. wheeleri*

***Angelica kingii* (Wats.) Coult. & Rose** Great Basin Angelica. [*Selinum kingii* Wats.]. Plants (3) 4–12 dm tall, glabrous except scabrous to short-hispid in the inflorescence, from a taproot, without persisting leaf bases; leaves ternate-pinnate with 4–5 (6) opposite pairs of lateral primary leaflets, the lower pairs mostly pinnate, lower petioles to 25 cm long, dilated at the base, the upper ones reduced, lower blades to 40 cm long, oblong in outline, the upper ones reduced; lowest pair of primary leaflets about 2/3–3/4 as long as the leaf blade, ascending and more or less parallel to the primary rachis, on petiolules 3.5–12 cm long; leaflets 2–14 cm long, 4–15 (40) mm wide, lanceolate to nearly linear, coarsely toothed or lobed, the margins with 1–3 teeth or lobes per cm or rarely entire; peduncles mostly 4–17 cm long; umbels 3–7; involucre lacking; rays 11–20, 1.5–9.5 cm long, scabrous; involucels lacking; pedicels 1–6 mm long, scabrous or short-hispid; petals white, sometimes marked with purple in age; stamens white; styles to about 1.5 mm long; fruit 4–5 mm long, densely hispid, the ribs slightly winged, the lateral wings a little wider than the dorsal ones. Aspen-fir and streamside communities at 2,130 to 2,380 m in the Deep Creek Mountains, Juab County; Nevada, eastern California, and southern Idaho; 5(0).

***Angelica pinnata* Wats.** Small-leaved Angelica [*A. leporina* Wats.]. Plants 4.5–10 (15) dm tall, glabrous or nearly so except scabrous to hirtellous in the inflorescence, without persistent leaf bases, from a taproot and sometimes branched crown; leaves pinnate or partly bipinnate with 3 (4) opposite pairs of leaflets, the lowest pair sometimes bipinnate or partly bipinnate, the upper pairs pinnate, lower petioles 5–26 cm long, gradually expanded into a dilated, partly sheathing base, the upper ones reduced and the blades sometimes sessile on the dilated sheath, blades (5) 9–21 cm long, more or less oblong in outline; leaflets 1.5–13 cm long, 4–37 mm wide, sessile, mostly lanceolate, occasionally elliptic, rarely ovate, finely to coarsely serrate, the margins with about 3–7 teeth per cm; peduncles 3.5–14 cm long; umbels (1) 2–5; involucre lacking; rays 7–14, 2–8.5 cm long, usually scabrous to hirtellous; involucels lacking or very rarely of 1 or more green to scarious linear or nearly linear bractlets to 3 (13) mm long; pedicels 3–7 mm long, glabrous or scabrous; petals white; styles to about 1 mm long; ovary glabrous to hirtellous; fruit 4–5 mm long, glabrous or sparsely hirtellous, the lateral wings about 1 mm wide, the dorsal wings about 0.5 mm wide. Tall forb, oak, maple, aspen, Douglas-fir, spruce-fir, willow, and wet meadow communities, very often along streams or around seeps and springs at 1,520 to 3,290 m in all Utah counties except Box Elder, Carbon, Millard, Morgan, and Rich; eastern Idaho to western Montana, south to Utah and Colorado; 65 (xv).

***Angelica roseana* Henderson** Rock Angelica. Plants 30–75 cm tall, strongly aromatic, glabrous or scabrous in the inflorescence, from stout taproots; stems stout, hollow, often 1–2 cm in diameter; leaves ternate-pinnate with 3–4 opposite pairs of lateral primary leaflets, the lower pairs bipinnate or ternate and petiolulate, the upper pairs pinnate and sessile; petioles to 8 cm long or lacking on the upper leaves and then blades sessile on a dilated sheath; blades 5–17 cm long, ovate in outline, the upper ones reduced to lacking and leaves reduced to dilated sheaths; lowest pair of primary leaflets about 3/4 as long as the leaf blade, on petiolules 2.5–5.2 cm long, blades of leaflets (1) 2–5 cm long, ovate to orbicular, sharply serrate-dentate, rarely lobed; peduncles 4–17 cm long, the terminal one often about as thick as the stem, the lateral ones often partly enveloped in bladeless, dilated sheaths; umbels 1–3; involucre lacking or occasionally of 1–2 linear bracts to 1.5 cm long; rays 15–30, 3.5–12 cm long, scabrous; bractlets of the involucel 1–3 (rarely more), 3–10 mm long, 0.2–0.5 mm wide, separate, linear; pedicels 4–9 mm long, glabrous or scabrous; petals white; stamens whitish; styles about 2 mm long; ovary glabrous or at most scabrous; fruit ca 5 mm long, the ribs with wings about 1 mm wide. Talus slopes, boulder fields, rock stripes, and rocky ground, above timberline or upper spruce zone at (3,050) 3,200 to 3,570 m across the Uinta Mountains and Mount Timpanogos of the Wasatch Range in Daggett, Duchesne, Summit, Uintah, and Utah counties, Montana to Idaho, south to Colorado and Utah; 14 (iii).

***Angelica wheeleri* Wats.** Utah Angelica. [*A. dilatata* A. Nels. in Coult. & Rose]. Robust plants 1–2 m tall or taller, glabrous except in the inflorescence, mildly if at all aromatic, from stout rootcrowns with large fibrous roots; stems hollow, to 3 cm in diameter; lower leaves ternate-pinnately compound, with 3–5 opposite pairs of lateral primary leaflets, the lower pairs bipinnate or tripinnate and petiolulate, the upper pairs often pinnate and sessile, petioles to 45 cm long, often dilated, blades to 40 cm long, ovate in outline; lowest pair of primary leaflets to 21 cm long, about 1/2 as long as the leaf blade, on petiolules to 5 cm long, blades of leaflets 3–16 cm long, 2–8 cm wide, lanceolate to ovate, serrate and some usually lobed; peduncles 2–29 cm long, often subtended by bladeless or nearly bladeless, dilated sheaths 2–20 cm long; umbels several; involucres lacking or occasionally of 1–2 linear bracts to 2 cm long; rays 20–45, 5–10 cm long, scabrous; involucels none; pedicels 5–12 mm long, glabrate to scabrous-hirsute; petals white; stamens whitish; styles about 1 mm long; ovary and young fruit scattered to densely hispid to hirsute, mature fruit 4–5 mm long, densely hispid, the dorsal and lateral ribs conspicuously winged. Boggy or very wet areas often in riparian communities or in seeps and springs at 1,950 to 3,050 m in Cache, Juab, Piute, Salt Lake, Sevier, and Utah counties; endemic to Utah; 7 (ii). *A. arguta* Nutt. in T. & G. has been reported for Utah, but I have not seen a specimen and suspect that reports are based on *A. wheeleri*. It is apparently different from *A. wheeleri* only in the glabrous ovaries and fruit.

Berula Hoffm.

Perennial, caulescent, glabrous herbs from fibrous roots, often stoloniferous; leaves pinnately compound or the submerged ones sometimes with filiform-dissected blades; umbels compound; involucre and involucel usually well developed; calyx teeth minute or obsolete; stylopodium conic; carpophore divided to the base, inconspicuous, adnate to the mericarps; fruit elliptic to orbicular, somewhat compressed laterally, glabrous, the ribs inconspicuous.

***Berula erecta* (Huds.) Cov.** Cutleaf Waterparsnip. [*Sium erectum* Huds.]. Stems 5–10 dm long or longer, from numerous fibrous roots; leaves pinnate with (3) 5–15 opposite pairs of lateral leaflets, or the submerged leaves (if present) often with filiform-dissected blades, petioles to 32 cm long or upper blades sessile on a dilated sheath, blades 2–31 cm long; leaflets 0.3–4 (6.5) cm long, sessile, nearly linear to lanceolate or ovate in outline, toothed to incised or occasionally a few entire; peduncles 1.5–8 cm long; umbels 3–20 or more; bracts of the involucre 1–6, 2–15 (25) mm long, linear or elliptic, entire, toothed, or rarely pinnatifid; rays 4–16, 0.5–2.5 (4) cm long; bractlets of the involucels ca 4–7, 1–7 mm long, linear or elliptic, entire; pedicels 2–7 mm long; petals white; stamens white; styles less than 1 mm long; fruit ca 2 mm long, the ribs obscure. In mud and water of streams, seeps, springs, marshes, swamps, margins of ponds and lakes, and in wet hanging gardens at 850 to 2,130 m in all counties of the state except Daggett, Emery, Grand, Iron, Morgan, San Juan, Summit, and Wayne; widespread in Europe, Mediterranean regions, and North America. The American plants are referable to var. *incisa* (Torr.) Cronq.; 64 (vi).

Carum L.

Biennial, caulescent, glabrous herbs from taproots; leaves pinnately compound; inflorescence of compound umbels; involucre and involucel lacking or of a few inconspicuous bracts or bractlets; calyx teeth obsolete; stylopodium low conic; carpophore divided to the base; fruit oblong to broadly elliptic-oblong, somewhat compressed laterally, evidently ribbed.

***Carum carvi* L.** Caraway. Plants 3–6 (10) dm tall; leaves 2–3 times pinnate and then often pinnatifid, with about 6–11 opposite or offset pairs of lateral primary leaflets, petioles to 15 cm long, the upper ones reduced and the blades sometimes sessile on a dilated sheath, the blades 5–16 cm long, oblong in outline; primary leaflets from less than 1/4 to about 1/2 as long as the leaf blade, sessile, the ultimate segments 2–8 (15) mm long, 0.5–2 mm wide, linear and entire or obovate and toothed to lobed; peduncles 4–12 cm long, usually subtended by a dilated sheath; umbels 6–12 or more; involucre lacking or inconspicuous; rays 6–12 (14), 1.5–8 cm long; involucels lacking or of minute scarious teeth; pedicels (5) 8–20 mm long; petals white; filaments white, the anthers pale green or whitish; styles about 0.5–0.85 mm long; fruit 3–4 mm long, the ribs filiform. Introduced, cultivated, the fruits used in flavoring, escaping, and occasionally persisting in mountain brush, meadow and aspen communities, at 1,375 to 2,640 m in Box Elder, Cache, Daggett, Davis, Duchesne, Salt Lake, Sanpete, Sevier, and Summit counties; native to Eurasia, now widespread across the United States; 10 (iv).

Cicuta L.

Perennial, caulescent, glabrous, violently poisonous herbs, from clusters of fibrous roots, some of these generally tuberous-thickened; base of stem thickened, with hollow chambers separated by transverse septa; internodes of stems hollow; leaves 1–3 times pinnate or ternate-pinnate, with well developed leaflets (ours); umbels several, compound; involucre wanting or of a few inconspicuous narrow bracts; involucel of several narrow bractlets or rarely lacking; petals white or greenish; calyx teeth evident; stylopodium depressed or low-conic; carpophore divided to the base, deciduous; fruit ovate or orbicular, compressed laterally, the ribs usually prominent and corky.

***Cicuta maculata* L.** Water Hemlock. [*C. douglasii* (DC.) Coult. & Rose, misapplied - the name belongs to plants north and west of Utah]. Plants, 6–21 dm tall or taller, with clusters of fibrous roots surmounted by a thickened crown; stems 5–15 mm or more in diameter; leaves pinnate or ternate-pinnate with 4–7 opposite pairs of lateral primary leaflets, the lower pairs again pinnate, the upper pairs once pinnate and sessile, lower petioles about 5–40 cm long, the upper ones reduced and the blades often sessile on dilated sheaths, lowest pair of petiolules 1–3 cm long, leaflets 2–11 cm long, 3–25 mm wide, narrowly lanceolate to lanceolate or occasionally linear, finely to coarsely serrate; peduncles (2) 4–15 cm long; umbels 6–30 or more; involucre lacking or of 1 or few linear bracts to 1 cm long; rays 15–26, 1.5–4 cm long; bractlets of the involucels about 6, 1–4 mm long, linear or narrowly deltoid, pale yellow-green or purplish, scarious-margined; pedicels 3–10 mm long; calyx teeth about 0.5 mm long, often pale green with whitish margins; petals white; stamens white; styles 0.5–1 mm long; fruit 2–4 mm long, oval to globose, the ribs prominent, more or less corky, green, often wider than the darker (often purple) intervals. Along streams, rivers, ditches, canals, margins of pond and lakes, in wet meadows and marshes at 1,370 to 2,320 m in Beaver, Cache, Daggett, Duchesne, Kane, Millard, Piute, Salt Lake, San Juan, Sanpete, Summit, Tooele, Uintah, Utah, Wasatch, Washington, Wayne, and Weber counties; widespread in North America; 46 (v.) Some of our plants have leaflets less than 5 times as long as wide (a feature of var. *maculata*, which is found mostly east of Utah), but in these specimens, as well as others from the state, the styles are not more than 1 mm long. All Utah specimens I have seen belong to var. *angustifolia* Hook., the common phase in western North America.

Conioselinum Hoffm.

Perennial more or less caulescent herbs from a taproot or cluster of fleshy-fibrous roots, sometimes with a caudex; leaves pinnately or ternate-pinnately decompound; inflorescence of compound umbels; involucre lacking or of a few narrow or leafy bracts; involucels of well-developed, narrow, often scarious bractlets; calyx teeth obsolete; petals white; stylopodium conic; carpophore divided to the base or nearly so; fruit elliptic or elliptic-oblong, slightly dorsally compressed, glabrous, the lateral ribs evidently thin-winged, the dorsal ribs less so and corky.

Conioselinum scopulorum **(Gray) Coult. & Rose** [*Ligusticum scopulorum* Gray]. Plants perennial 3–10 dm tall, glabrous except in the inflorescence, from a fusiform taproot with simple or sparingly branched crown, without persisting leaf bases or these few and weakly persisting; leaves pinnate or ternate-pinnate with (3) 4–5 opposite pairs of lateral primary leaflets, the lower pairs 2–3 times pinnate and petiolulate, the upper pairs pinnate and pinnatifid and sessile or nearly so, petioles 3–23 cm long, blades 3.5–19 cm long, ovate in outline, lowest pair of primary leaflets 1/2–2/3 as long as the leaf blade; on petiolules (0.5) 1–3.5 cm long, ultimate segments 2–15 mm long, 1–5 mm wide; peduncles 3–21 cm long, often subtended by a dilated sheath, this usually with a reduced sessile blade; umbels 1–3; involucre lacking or of 1 or few linear bracts to 1 cm long; rays 9–15, 1.5–5 cm long; involucels of 3–6 linear or linear-filiform bractlets 2–8 mm long; pedicels 4–12 mm long; petals white; stamens white; styles to about 1.3 mm long; fruit 4–6 mm long, lateral ribs narrowly corky winged, the dorsal ones not winged. Apparently rare, along streams at 2,550 to 3,200 m in Daggett, Grand, Garfield, Piute, San Juan, Summit, and Wayne counties; Wyoming to Arizona and New Mexico; 18 (iii). Plants of *C. scopulorum* are often confused with those of *Ligusticum porteri*. The two taxa differ in the following subtle ways, with features of *L. porteri* in parentheses; fruit dorsally flattened (nearly terete); bractlets of the involucel often 3 or more (0–2, rarely more); terminal umbel solitary or subtended by alternate lateral umbels (often subtended by opposite or whorled umbels); and plants from a taproot, with a mostly simple crown and with few if any persisting fibrous leaf bases (the crown simple or branched and often with numerous, persistent, fibrous leaf bases). In addition, the rays average shorter and the ultimate segments of the leaves are less conspicuously veined than in those of *L. porteri*.

Conium L.

Biennial caulescent glabrous herbs from stout taproots with purple-spotted, freely branching hollow stems; leaves pinnately or ternate-pinnately dissected; umbels compound, several or numerous; involucre and involucels of small, lanceolate to ovate bracts or bractlets; calyx teeth obsolete; petals white;

stylopodium depressed conic; carpophore entire; fruit broadly ovoid, somewhat laterally compressed, with prominent, raised, often wavy slightly winged ribs.

Conium maculatum **L.** Poison Hemlock. Plants 5–30 dm tall, glabrous, violently poisonous; leaves pinnate or ternate-pinnately decompound with 6–9 opposite pairs of lateral primary leaflets, the lower pairs usually twice or more pinnate and then pinnatifid, petiolulate, the upper pairs once pinnate and pinnatifid and sessile, petioles of larger leaves 4–18 cm long; larger leaf blades to 30 cm long, reduced upward and sessile on dilated sheaths, ovate in outline; lowest pair of primary leaflets less than 1/2 to 2/3 as long as the leaf blade, on petiolules 1–5.5 mm long or those of upper leaves shorter; ultimate leaflets pinnatifid, the lobes entire or toothed, the widest confluent portions 2–5 (10) mm wide; peduncles 2–7.5 cm long; umbels many; involucral bracts 2–6, 2–6 (15) mm long, entire and ovate or ovate-caudate or ovate-cuspidate to deltoid, green with scarious margins, or rarely pinnatifid; rays 9–16, 1–4 cm long; bractlets of the involucels 4–6, 1–3 mm long, shaped like the involucral bracts; pedicels 2–6 mm long; petals white; stamens white; styles about 0.5 mm long; fruit 2–2.5 mm long, the ribs prominently ridged, narrower than the intervals. Along ditches, streams, rivers, roadsides, and fence lines, in wet and boggy meadows and moist waste places at 1,400 to 2,135 (2,990) m in Box Elder, Cache, Davis, Duchesne, Juab, Rich, Salt Lake, Sanpete, Summit, Tooele, Uintah, Utah, and Weber counties; introduced from Eurasia, now widespread in North America; 34 (iv).

Cymopterus Raf.

Perennial, acaulescent or subcaulescent, glabrous or scabrous herbs from slender to greatly enlarged and tuberlike taproots to branching woody caudices; leaves all basal (these sometimes elevated on an aerial pseudoscape) or basal and 1–few cauline mostly on the lower 1/2 of the stems, ternate to pinnate or ternate-pinnately compound, rarely simple and ternately cleft; umbels solitary to several, open or reduced to globose heads; involucres lacking or well developed; involucels of separate or united bractlets; pedicels obsolete to well developed; calyx teeth obsolete to conspicuous; petals white, yellow, or purple; stylopodium lacking; carpophore lacking, inconspicuous and adhering to the inner faces (commissure) of the mericarps , or well developed and persistent on the pedicel and divided to the base; fruit ovoid to oblong, somewhat flattened dorsally, the lateral and usually 1 or more of the dorsal ribs prominently winged. The strongly aromatic members of the group with woody branched caudices and greenish acute conspicuous calyx teeth have been included in the genus *Pteryxia*. These plants typically have leaves with 6–10 opposite pairs of lateral primary leaflets. Most of those in *Cymopterus* are ternate or have only 2–6 opposite pairs of lateral primary leaflets. However, the caudex and sometimes the number of primary leaflets are repeated in *C. bipinnatus* Wats., *C. aboriginum* Jones, and in other taxa long included in *Cymopterus*. If high volatile oil content is unique to taxa of the *Pteryxia* group, this feature, in combination with others might warrant generic segregation. Chemical studies might prove useful in resolving this problem.

1. Leaves 1 or 2 times pinnate or a few merely ternate, with entire (rarely bifid) linear or linear-elliptic leaflets 0.5–4 (5.5) cm long and 1–2 (3) mm wide; plants caulescent, of Wayne and San Juan counties, rare .... *C. beckii*

— Leaves not as above in all features; plants acaulescent or subcaulescent with 1–3 leaves mostly on the lower 1/3 of the stem 2

2(1). Peduncles rather densely hirtellous just below the umbel, mostly glabrous elsewhere; leaves mostly twice pinnate with 2–4 opposite pairs of mostly trifid or pinnatifid primary leaflets, the primary leaflets all sessile or the lower pairs on petiolules to 15 mm long; plants not aromatic, sometimes with 1 or 2 cauline leaves, montane, mostly above 2,400 m .... *C. lemmonii*

— Peduncles not hirtellous just below the umbel, sometimes scabrous but then not more so just below the umbel than elsewhere; leaves various but seldom with the above combination of features; plants various 3

3(2). Plants strongly aromatic, from a branched more or less woody caudex, mostly clothed at the base with long-persisting leaf bases and sometimes stem bases, often of rocky places; leaves with (4) 6–10 opposite or offset pairs of lateral primary leaflets, completely and finely dissected so that the ultimate segments (0.3–1.5 mm wide) are the widest undivided parts of the blade; calyx teeth rather prominent, about 0.5–1 mm long, acute, greenish (*Pteryxia* group) 4

— Plants not strongly aromatic, from fibrous taproots with simple or sparingly branched crowns, without or with few persisting leaf bases, not specific for rocky places; leaves once ternate to pinnately decompound with 2–6 opposite or offset pairs of lateral primary leaflets, sometimes not completely dissected, confluent portions of blades sometimes broader than the ultimate teeth or lobes; calyx teeth to about 0.5 mm long, rarely acute . 5

4(3). Lowest pair of primary leaflets (1/5) 1/2–3/4 or more the length of the leaf blade, mostly 3–9 cm long, several times longer than the upper pairs, on petiolules 2–4 cm long; stems frequently with 1 or 2 cauline leaves on the lower 1/3; fruiting styles (2.5) 3–4 mm long, mostly curved or coiled; involucels 2–5 mm long, not exserted beyond the flowers; plants growing 1,400–2,320 (2,560) m ...... *C. terebinthinus*

— Lowest pair of primary leaflets 1/4 or less the length of the leaf blade, to 2.7 cm long, often not more than twice as long as some of the upper pairs, sessile or on petiolules to 1 cm long; leaves strictly basal; fruiting styles to 2 (2.5) mm long, straight or nearly so, bractlets of involucels 2–10 mm long, some often exserted beyond the flowers; plants growing at (very rarely 2,285) 2,740–3,660 m .... *C. hendersonii*

5(3). Involucels scarious, purplish or whitish with purple nerves, the bractlets mostly over 3 mm wide, sometimes united to midlength; involucres like the involucels but larger or sometimes reduced or lacking; broadest wings of the fruit (2) 3–7 mm wide 6

— Involucels greenish or the bractlets very narrow and divided to the base or nearly so; involucres lacking; broadest wings of the fruit to 2.5 mm wide or to 5.5 in *C. purpureus* 8

6(5). Rays 1–3.5 cm long, usually at least some exceeding the well- developed to obsolete involucre through all stages of phenology, not obscured by the dense mature fruits; lobes of the involucre and involucel not multinerved; carpophore well developed, tending to persist on the pedicels after the mericarps have fallen; fruit often oblong in outline, the wings 1.7–3(4) mm wide; plants of the Colorado drainage .... *C. bulbosus*

— Rays 0.3–1 cm long, rarely longer, not exserted beyond the always well-developed involucre, or if exserted then the lobes of the involucre and involucel multinerved, obscured by the dense mature fruits; carpophore lacking or hairlike and more or less adhering to the faces of the mericarps and not persistent on the pedicels; fruit ovate to orbicular in outline, the wings 3–7 mm wide; plants of the Great Basin and Colorado drainage 7

7(6). Lobes of the involucels and usually of the involucres with more than 3 parallel purplish nerves that extend to or near the tip; involucre sometimes reduced to a ring; plants of Kane and Washington counties .... *C. multinervatus*

— Lobes of the involucels and involucres with a midnerve extending to the tip and sometimes 1 or 2 lateral shorter nerves extending to about midlength or less; involucre well developed; plants widespread ..... *C. purpurascens*

8(5). Involucels green and of the same texture as the leaves, seldom scarious-margined, the bractlets mostly 1.5–4 mm wide, plants mostly obscurely viscid and dotted with numerous adhering grains of sand especially on the scapes and petioles, growing at 850–1,890 m 9

— Involucels rarely wholly green, not of the same texture as the leaves, often scarious-margined and/or the bractlets linear or narrowly elliptic and not over 1.5 mm wide; plants not viscid, rarely with numerous adhering grains of sand, sometimes growing above 1,890 m 10

9(8). Leaves once ternate, the 3 leaflets ternately lobed or cleft, the blades with confluent portions 5–35 mm wide; outer rays 1–3.3 cm long; bractlets of involucel entire or rarely tridentate; pseudoscape lacking; plants of the southern 1/2 of the state .... *C. newberryi*

— Leaves 2–3 times pinnate with 2 (3) opposite pairs of lateral primary leaflets, some rarely ternate, the blades with confluent portions 1–7 (12) mm wide, rays to 1.3 cm long; bractlets of the involucel often with 2–3 teeth; pseudoscape often present; plants widespread .... *C. acaulis*

10(8). Carpophore lacking; pedicels obsolete or to 1 mm long; rays obsolete or short and concealed in the very dense fruits of a globose headlike inflorescence; styles less than 1 mm long, or if rays evident (to 17 mm long) and styles to 2 mm long then leaves ternate without a rachis and with lobes sharply dentate-serrate; plants endemic to the Great Basin, not found above 1,980 m 11

— Carpophore well developed, divided to the base; pedicels mostly over 1 mm long; rays short or rather long, not concealed in the dense inflorescence; styles mostly 1–3 mm long; leaves 2–3 times pinnate or if ternate then usually with a rachis and lobes not dentate-serrate; plants of broad distribution, those with rays less than 17 mm long often found above 1,980 m 13

11(10). Leaves pinnate with 2–3 pairs of lateral primary leaflets, rarely some ternate, the blades narrowly ovate to oblong in outline; rays and pedicels obsolete; inflorescence a dense globose head; wings of fruit more or less spongy thickened; styles 0.5–0.8 mm long; anthers white .... *C. globosus*

— Leaves ternate or occasionally simple and ternately cleft, the blades reniform, orbicular, to ovate in outline; rays and sometimes pedicels more or less evident when young, inflorescence various; wings of fruit papery; styles various; anthers yellowish or purplish 12

12(11). Leaves 2 and opposite, rarely 3, the ultimate lobes crenate; pseudoscape solitary, subterranean; peduncles solitary; rays 3–10 mm long, hidden at maturity in the very dense globose headlike umbel; styles about 0.4 mm long; plants of Juab, Sanpete, and Sevier counties . . . . *C. coulteri*

— Leaves often more than 2, the ultimate lobes dentate; pseudoscapes or stems rarely solitary; peduncles 1–4 (6); rays 8–17 mm long, not hidden as above, the umbel not globose and headlike; styles 1.5–2 mm long; plants of Beaver and southwestern Millard counties . . . . *C. basalticus*

13(10). An aerial pseudoscape rather quickly developing, (3.5) 5–24 cm long; leaf blades with 4–6 opposite or offset pairs of lateral primary leaflets; umbels sometimes nodding on recurved peduncles; petals white or yellow, seldom turning light purple; plants mostly montane in central and western Utah 14

— Pseudoscape lacking or mostly subterranean, the aerial portion not over 3 cm long; leaf blades with 2–4 opposite pairs of lateral primary leaflets, or ternate; umbels not nodding; petals white or yellow, often turning dark purple 15

14(13). Leaves 3 times pinnate, finely and completely dissected, with the ultimate segments the widest undivided portions of the blades, these to 2 mm long and to 1 mm wide; upper primary leaflets not tending to be confluent with the rachis; petals white; anthers purple; plants of western Utah . . . . *C. ibapensis*

— Leaves 2 (3) times pinnate, the ultimate lobes or teeth 1–5 mm long, 0.5–3 mm wide, these often not as wide as the confluent portions of the blade that are up to 12 mm wide; upper primary leaflets tending to be confluent with the rachis, and pinnatifid or only lobed; petals yellow or white; anthers yellow or white; plants of northern and central Utah . *C. longipes*

15(13). Leaves once pinnately compound with 2 opposite pairs of lateral primary leaflets, or a few ternate or rarely biternate, glaucous, confluent portions of the blades (3) 6–25 (40) mm wide; petals and stamens bright yellow when fresh, fading to cream or white in herbarium specimens; plants of the Uinta Basin at 1,430–1,800 m . . . . *C. duchesnensis*

— Leaves ternate or 2–3 times pinnately compound with up to 4 opposite pairs of lateral primary leaflets, glaucous or not, the confluent portions mostly 1–4 mm wide or if wider then the leaves ternate; petals yellow, purple, or white when fresh, if yellow then turning dark purple in herbarium specimens; plants of broad distribution 16

16(15). Petals cream-pink to pale purple when fresh, with light or moderate purple markings in herbarium specimens; rays of the umbel 2–18 mm long; pedicels to 3 mm long; blades of leaves 1–3 cm long, pinnately dissected, the confluent portions rarely over 3 mm wide, plants scabrous, of Garfield, Iron, and Kane counties, at moderate to high elevations . . . . *C. minimus*

— Petals yellow or purplish when fresh, turning dark purple in herbarium specimens; rays, pedicels, and leaves mostly longer than above or the leaves mostly ternate with confluent portions often 5–21 mm wide; plants widespread . . . . *C. purpureus*

Cymopterus acaulis **(Pursh) Raf.** Plains Spring-parsley. [*Selinum acaule* Pursh]. Plants 5–18 (27) cm tall, from a simple or rarely branched, deep seated, nearly linear or slightly to much enlarged fibrous taproot; herbage often more or less viscid and dotted with sand grains; pseudoscapes 1–2 (3) per plant, 0.5–5.5 cm long, often partly or wholly subterranean; leaves basal or more often whorled with the peduncles atop the pseudoscape, occasionally 1 or 2 on a pseudoscape-like stem, 2–3 times pinnate, with (1) 2 (3) opposite pairs of lateral primary leaflets; petioles 2–8 (11) cm long, blades (1)2–5.5 (7) cm long, the confluent portions 1–7(12) mm wide, oblong, ovate, to nearly linear in outline; primary leaflets 5–35 mm long, gradually reduced upward, pinnate to bipinnatifid with few to several rounded to narrow lobes, the ultimate teeth or lobes to 10 (16) mm long, to 2 mm wide; peduncles 1–14, (1.5) 3–14 (19) cm long; involucres lacking; rays about 6–9, about 1–13 mm long; bractlets of the involucel 3–8 (11) mm long, ca 1.5–4 mm wide, more or less united at the base, entire or with 2–3 teeth or lobes, green or purple in age, of the texture of the leaves; pedicels to 2 mm long; calyx teeth ca 0.2 mm long, greenish; petals white, yellow, or purple; stamens the color of the petals; styles ca 2.5 mm long; carpophore lacking; fruit 5–10 mm long, the wings slightly longer than the body, to 2 mm wide, slightly corky, some of the dorsal ones sometimes obsolete. With 4 more or less intergrading varieties in the state.

1. Petals and stamens yellow when fresh, sooner or later fading to white or cream when dried 2

— Petals and stamens white or purple when fresh 3

2(1). Peduncles mostly shorter than the leaves, to ca 4 cm long; wings of the fruit mostly strongly wavey and often erose, to 7 mm long; leaf blades to about 4 cm long; plants seldom over 7 cm tall, of the Great Basin . . . . *C. acaulis* var. *parvus*

— Peduncles equaling or exceeding the leaves, to 14 (19) cm long; wings of the fruit straight or slightly wavey, mostly entire or obscurely erose, to 10 mm long; leaf blades to 7 cm long; plants often over 7 cm tall, of the Colorado Basin . . . . *C. acaulis* var. *fendleri*

3(1). Petals and stamens purple; peduncles mostly exceeding the leaves; plants of Kane County . . . . *C. acaulis* var. *higginsii*

— Petals and stamens white; peduncles mostly shorter than or equalling the leaves; plants of Daggett County and the Uinta Basin . . . . *C. acaulis* var. *acaulis*

Var. *acaulis* Desert shrub, sagebrush, and juniper communities at 1,432 to 1,980 m in Daggett, Duchesne, and Uintah counties; Saskatche-wan and Minnesota west to Oregon and south to Texas and northern Utah; 21 (vi). Plants with white flowers grow among those with yellow flowers in the Uinta Basin, where it is difficult if not impossible to recognize two taxa. Even when fresh the white flowers do not seem as bright as those of Wyoming, and the Uinta Basin materials seem transitional to var. *fendleri*.

Var. *fendleri* (Gray) Goodrich, comb. nov. [based on: *C. fendleri* Gray Mem. Amer. Acad. II. 4: 56. 1849; *C. decipiens* Jones, type from Cisco]. Desert shrub, blackbrush, sagebrush, and pinyon-juniper communities often on sandy soil at 1,885 to 1,890 m in Duchesne, Carbon, Emery, Garfield, Grand, Kane, San Juan, Uintah, and Wayne counties; Utah and Arizona; 74 (v). This taxon has long been separated at the species level from *C. acaulis*. The rather recent discovery of intermediate plants in the Uinta Basin and of other yellow-flowered varieties (var. *parvus* from the Great Basin and var. *greeleyorum* Grimes & Packard of Oregon) greatly weaken the case for such separation.

Var. *higginsii* (Welsh) Goodrich, comb. nov. [based on: *C. higginsii* Welsh Great Basin Nat. 35: 377. 1976]. Desert shrub communities, often on sandy alluvium of Tropic Shale at about 1,525 m in Kane County; endemic; 4 (0). The color of the petals persists as a bright purple long following collection, and the color marks this variety as distinct from any in the complex.

Var. *parvus* Goodrich, var. nov. Similis *Cymopterus acaulis* var. *acaulis* sed parvioribus saepe, petalis flavis et alis fructus undulatis et erosis valde differt, sed similis var. *fendleri* in floribus flavis et var. *acaulis* in scapis brevis. HOLOTYPE: Utah. Tooele Co., 32.7 km 326 degrees NW of Vernon. Skull Valley-Stansbury Mtns., T6S, R7W, Sec 32, near 1/4 corner with Sec 33, 1,585 m. Juniper-big sagebrush community, stabilized aeolian sand, 7 June 1984, S. Goodrich 20458 (BRY); isotypes UC, NY, RM, CAS, POM, UTC, UT, US. Additional specimens: Tooele Co., Ibid., 7 May 1984, S. Goodrich 20251 (BRY; UT, RM, NY, UTC). Desert shrub, sagebrush, and juniper communities, often on aeolian sand, at 1,400 to 1,585 m in Millard and Tooele counties; endemic; 15 (xii). This variety is similar to var. *acaulis* in the short scape, but differs in the yellow flowers. It is similar to var. *fendleri* in the yellow flowers but differs in the short scapes, and it is similar to the extralimital var. *greeleyorum* Grimes & Packard in the short scape and yellow flowers but apparently most closely related to the latter taxon. It differs from var. *greeleyorum* in the strongly undulate, erose wings of the smaller fruit. Fruiting material of var. *greelyorum* was loaned through the kindness of Dr. Patricia Packard.

***Cymopterus basalticus* Jones** Dolomite Spring-parsley. Plants 4–15 cm tall, from a taproot with simple or branched crown, glabrous, glaucous, with 1–few mostly etiolated, subterranean, short pseudoscapelike stems; pseudoscape mostly lacking, if present short and enveloped in bladeless sheaths, the crown sometimes with a few long-persisting leaf bases; leaves basal, (2) 3–9 per plant, ternately divided without a rachis, or occasionally simple and ternately cleft, petioles 1.5–5 cm long, blades 1–3.5 cm long, orbicular to reniform, confluent portions 4–32 mm wide; leaflets 5–30 mm long, sessile, orbicular, ternately lobed, the major lobes again lobed, mostly ternately so, the ultimate lobes coarsely dentate; peduncles 1–4 (6) per plant, 3.5–8 (14) cm long; involucre lacking; rays 6–14, 8–17 mm long, usually evident in fruit; bractlets of the involucel 6–8, 2–5 mm long, more or less united at the base, white, pink, or purplish with white scarious margins; pedicels obsolete or nearly so; petals white or purplish; stamens yellowish or purplish;

styles 1.5–2 mm long; carpophore lacking; body of fruit 3–6 mm long, the wings 4–7 mm long, 1–2 mm wide, whitish, papery, some of the dorsal ones often reduced. Desert shrub communities, gravelly hills and alluvial fans mostly of dolomite substrate, at 1,705 to 1,985 m in western Beaver and Millard counties; Utah and adjacent White Pine County; Nevada, a rather narrow Great Basin endemic; 21 (v). The orbicular to reniform leaf blades without a rachis are unique in the genus.

***Cymopterus beckii* Welsh & Goodrich** Pinnate Spring-parsley. Plants 20–40 cm tall, glabrous, weakly if at all aromatic, caulescent with leaves extending well up the stem, from a taproot with a simple or sparingly branched crown, often clothed at the base with long-persisting leaf bases; leaves 1 or 2 times pinnate, with 2–3 opposite pairs of lateral leaflets, or the upper ones sometimes ternate, petioles 2–13 cm long, blades 2–10 cm long; leaflets 3–7, 0.5–4 cm long, or the terminal one to 5.5 cm long, 1–2 (3) mm wide, sessile, linear or linear-elliptic, entire or rarely a few bifid; peduncles 4–8 (19) cm long; umbels 1–3 per stem; involucres lacking; rays 6–11, 0.6–1.4 cm long; bractlets of the involucels about 5, 1–5 mm long, to 1 mm wide, greenish or with narrow scarious margins, mostly separate; pedicels 1–3 mm long; petals and stamens bright yellow when fresh, fading whitish when dried (whitish within 2 years in herbarium specimens); styles 1.2–2.2 mm long; carpophore weak, adhering to the mericarps; fruit 6–8 mm long, oblong, the lateral wings to about 1 mm wide, the dorsal ones narrower, some often obsolete. Sandy or stoney places, pinyon-juniper-mountain brush communities at 1,700 to 2,150 m in San Juan and Wayne counties; endemic; 8 (iv). Apparently closely allied to *C. lemmonii*, but differing in entire leaflets, glabrous peduncles and rays, and the slightly longer fruit.

***Cymopterus bulbosus* A. Nels.** Onion Spring-parsley. Plants 8–27 cm tall, glabrous, glaucous, from a stout, thickened, often bulbous, fibrous taproot with a simple or sparingly branched crown; pseudoscapes obsolete or 1–2 (3), to 6.5 cm long and often partly or wholly subterranean, enveloped in dilated bladeless sheaths; leaves few to several, basal or whorled atop the pseudoscape with the peduncles, rarely 1 or 2 cauline, (1) 2–3 times pinnate, with (2) 3–6 opposite or offset pairs of lateral primary leaflets, the upper pairs often once-pinnate and more or less confluent, blades 2–10 cm long, ovate to oblong or nearly linear, confluent portions 1–5 mm wide, lowest pair of primary leaflets to 4 cm long, sessile or on petiolules to 2(5) mm long, the other primary leaflets progressively reduced upward, ultimate lobes and teeth 1–8 (12) mm long, about 1–4 mm wide, more or less rounded; peduncles (1) 3–8 (11) per pseudoscape, 4–18 cm long; involucre obsolete or reduced to a ring or cup, or the bracts well developed, to 13 mm long, translucent, white, more or less united, with a green midrib and occasionally 1 or 2 lateral nerves that extend to about 1/3 the length of the bract; rays 5–15, 1–3.5 cm long, usually exceeding the involucre at all stages of phenology; involucels 3–10 mm long, the bractlets more or less united at the base, similar in texture and color to the involucre, with a green center and midrib or the midrib sometimes purple, rarely with 1 or 2 lateral nerves extending to about midlength; pedicels 3–9 mm long; calyx teeth about 0.5–1 mm long, scarious, white, like the involucel, with a green midrib to about midlength; petals white, sometimes purplish in age; stamens white, or purple especially in age; styles about 2–4 mm long; carpophore divided to the base, more or less persistent on the pedicel after the mericarps have fallen; body of the fruit 6–11 mm long, to 2 (3) mm wide, the wings (7) 9–13 mm long, 1.7–3 (4) mm wide. Desert shrub and juniper communities at 1,220 to 2,005 m in the Colorado drainage in Carbon, Duchesne, Emery, Garfield, Grand, San Juan, Uintah, and Wayne counties; Wyoming to New Mexico and Arizona; 95 (xi). See *C. purpurascens*.

***Cymopterus coulteri* (Jones) Mathias** Two-leaf Spring-parsley. [*C. corrugatus* var. *scopulicola* Jones; *C. corrugatus* var. *coulteri* Jones; *Rhysopterus jonesii* Coult. & Rose]. Plants 4–11 cm tall, glabrous from a slightly to much enlarged fibrous taproot with simple crown, this giving rise to a solitary, mostly subterranean pseudoscape 2–6 cm long; leaves 2 (rarely 3 or 4 and the third and fourth ones usually smaller), opposite, borne at or near ground level, ternate or rarely simple and ternately cleft, petioles 1–3 cm long, blades 2–4 cm long, ovate to nearly orbicular in outline, confluent portions (5) 8–38 mm wide; leaflets 7–35 mm long, the lateral ones sessile mostly ternately lobed, the terminal on a winged more or less confluent rachis to 1 cm long, ternately cleft, the main lobes again lobed or crenate-toothed; peduncle solitary, 2–7 cm long; umbel globose, headlike, 1.5–5 cm across in pressed fruiting specimens; involucre lacking; rays 7–14 or perhaps more, 3–10 mm long, somewhat evident at anthesis, but hidden by the dense mature fruits; bractlets of the involucel 2–4 mm long, linear to narrowly ovate, green or purplish in age, often 3–nerved, with whitish or purplish scarious margins; pedicels shorter than the bractlets; calyx teeth minute but white and of the texture of the petals, deciduous; petals white; filaments white, anthers purple; styles (including the stigmas) ca 0.4 mm long; carpophore lacking; body of fruit 5–7 mm long, the wings 7–10 mm long, to about 2 mm wide, papery. Desert shrub, black sagebrush, and juniper communities, often on Arapien shale and other clayey and gravelly barrens or semibarrens at 1,540 to 1,700 m in Juab, Sanpete, Sevier, and Tooele counties; endemic; 28 (vii). The strong tendency for plants to have but 2 leaves is unique in the genus.

***Cymopterus duchesnensis* Jones** Uinta Basin Spring-parsley. Plants 7–23 cm tall, from a slender or more often enlarged bulbous taproot with simple or branched crown, glabrous and glaucous, not or weakly aromatic; stems short, often branched; pseudoscape lacking; leaves basal or 1–3 or more cauline, pinnate with 2 pairs of lateral leaflets, or occasionally a few ternate, or rarely biternate, petioles 2.2–11 cm long, blades (2) 3–10.5 mm long, ovate to oblong in outline, the confluent portions (3) 6–25 (40) mm wide; leaflets 1–5, on petiolules 2–32 mm long, ternately cleft or divided, the major lobes to 3 cm long, (3) 5–15 (20) mm wide, often again toothed or lobed and mostly ternately so, the ultimate teeth or lobes 1–8 mm wide; peduncles 1–3 per stem, 7–17 cm long; involucres lacking; rays 6–17, 1.5–4.4 cm long; bractlets of the involucel lacking or more often 1–7, 1–5 mm long, more or less united at the base, linear; pedicels (2) 4–9 mm long; petals and stamens bright yellow when fresh, fading to cream or greenish in herbarium specimens, not turning purple; styles 2–2.2 mm long; carpophore divided to the base, more or less persistent on the pedicel; body of fruit 5–9 mm long, the wings to 11 mm long, 2–2.5 mm wide, undulate to corrugated, more or less papery and not corky. Desert shrub, sagebrush, and juniper communities, sandy clay and clay semibarrens of Duchesne River, Mancos Shale, Morrison, Uinta, and Wasatch formations at 1,430 to 1,860 m, centered in Uintah County and also in eastern Duchesne County, Utah, and extreme western Moffat and Rio Blanco counties, Colorado; 47 (xiii).

***Cymopterus globosus* (Wats.) Wats.** Golfball Spring-parsley. [*C. montanus* var. *globosus* Wats.]. Plants 4–10 cm tall, from a slender or thickened fibrous taproot; pseudoscape (1) 2–6 cm long, all or nearly all subterranean, often loosely enveloped in dilated bladeless sheaths; leaves 1 or 2 atop the pseudoscape and some usually arising directly from the fibrous root and then with etiolated subterranean petioles, pinnate or bipinnate and then trifid or pinnatifid, with 2–3 opposite pairs of sessile lateral primary leaflets, or rarely ternate, petioles 1.5–6 cm long, blades 2–5 cm long, narrowly ovate to oblong, confluent portions 5–10 mm wide, lowest pair of primary leaflets 10–18 mm long, the ultimate lobes to 4 mm long, to 2 mm wide, mostly toothed; peduncles 1 or 2, 3–6 cm long; involucre lacking; umbel a globose head, the rays and pedicels obsolete; involucels concealed in the dense flowers and fruits; petals white; stamens white; styles 0.5–0.8 mm long; carpophore lacking; body of the fruit about 6 mm long, the wings ca 9 mm long, to ca 2.8 mm wide, wider toward the outside of the head, spongy thickened. Desert shrub communities at 1,400 to 1,525 m in Box Elder, Juab, Millard and Tooele counties; eastern California, Nevada, and western Utah; a Great Basin endemic; 6 (0).

***Cymopterus hendersonii* (Coult. & Rose) Cronq.** Mountain Rock-parsley [*Pseudoteryxia longiloba* Rydb.; *Pterxia hendersonii* (Coult. & Rose) Mathias & Const.; *Pseudocymopterus hendersonii* Coult. & Rose]. Plants (3) 5–34 cm tall, glabrous, strongly aromatic, from a branched woody caudex, clothed at the base with old petiole and peduncle bases, these sometimes persisting for a few or several years without shredding; leaves basal, bipinnate or occasionally partly tripinnate with 5–10 opposite or offset pairs of lateral primary leaflets, petioles (1) 2–14 cm long, blades (1) 1.5–10 cm long, oblong in outline, finely dissected so that the ultimate segments are the widest undivided parts of the blade, lowest pair of primary leaflets about 1/4 or less the length of the leaf blade, 5–27 mm long, sessile or on petiolules to 1 cm long, upper primary leaflets gradually reduced, the ultimate segments 1–12 mm long, 0.3–1.4 mm wide, acute, with a usually whitish tiny mucro; peduncles 7–30 cm long; umbels compact; involucres lacking; rays 6–16, 0.5–2.4 cm long, the inner ones shorter than the outer ones and often abortive; bractlets of the involucel 2–6, 2–10 mm long, linear, acute; pedicels 1–5 mm long; calyx teeth about 1 mm long, persisting in fruit, greenish, often reddish tinged, acute; petals and stamens bright yellow when fresh, fading whitish in herbarium specimens; styles to 2 (2.5) mm long; carpophore divided to the base; fruit 4–8 mm long, the wings to about 1 mm wide, some of the dorsal ones sometimes obsolete. Talus, cliffs, ledges, rocky spruce-fir, limber pine, and alpine communities at (2,285) 2,740 to 3,660 m in Beaver, Box Elder, Cache, Daggett, Duchesne, Grand, Juab, Piute, Salt Lake, San Juan, Sevier, Summit, Tooele, Uintah, and Utah counties; southwestern Montana and central Idaho, south to New Mexico; 66 (x).

***Cymopterus ibapensis* Jones** Ibapah Spring-parsley. [*C. watsonii* (Coult. & Rose) Jones]. Plants 7–25 cm tall, glabrous or granular-scabrous, not or weakly aromatic, from a linear taproot, this hardly if at all swollen, with a simple or occasionally branched crown; pseudoscapes 1–2 (5) per root, the aboveground portion 3.5–10 cm long, commonly enveloped at the base by scarious dilated bladeless sheaths; leaves whorled atop the pseudoscape, rarely some arising directly from the root, tripinnate, with 5–6 opposite or offset pairs of lateral primary leaflets, petioles (1) 1.5–3.5 cm long, blades (2.5) 4–11 cm long, ovate in outline, completely dissected so that the ultimate segments are the widest undivided portions of the blade; lowest pair of primary leaflets about 1/2 to over 3/4 as long as the leaf blade, sessile or on petiolules to 2 cm long, with 4–6 (8) opposite or offset pairs of secondary leaflets, the ultimate segments to 2 mm long, to about 1 mm wide; peduncles (2) 4–8 per pseudoscape, 2–15 cm long; umbels sometimes nodding on the sometimes recurved peduncles; involucre lacking; rays 10–18, 5–20 mm long; bractlets of the involucels to 4 mm long, to 0.5 mm wide, separate or nearly so, green with a purple midrib and narrow scarious margins; pedicels 4–6 mm long; calyx teeth to 1 mm long, greenish; petals white; filaments white, anthers purple; styles 1–2 mm long; carpophore divided to the base; body of fruit 5–8 mm long, the wings 6–9 mm long, to 2 mm wide, some of the dorsal ones sometimes reduced. Greasewood-sagebrush, sagebrush-grass, and pinyon-juniper communities at 1,520 to 2,755 m in Beaver, Box Elder, Iron, Millard, Piute, either or perhaps both Juab and Tooele, and Washington counties; southeastern Oregon, and Nevada; 30 (viii).

***Cymopterus lemmonii* (Coult. & Rose) Dorn** Spring-parsley. [*Pseudocymopterus lemmonii* (Gray) Coult. & Rose; *P. tidestromii* Coult. & Rose; *P. versicolor* Rydb.; *P. montanus* (Gray) Coult. & Rose; *Thaspium montanum* Gray; *Ligusticum montanum* (Gray) Gray]. Plants 8–50 cm tall, glabrous except on the peduncle and in the inflorescence, not or weakly aromatic, from a taproot with simple or branched crown, more or less clothed at the base with shredded persisting leaf bases; pseudoscape lacking; leaves basal and sometimes 1 or 2 cauline ones on the lower 1/3 of the stem and occasionally 1 on the upper 3/4, mostly bipinnate and then often bifid or pinnatifid in the lower part, with 2–4 opposite or offset pairs of lateral primary leaflets, rarely pinnate in part with entire leaflets; petioles 1–13 cm long, with a dilated base, blades (1) 2–8 cm long, confluent portions to 4 mm wide; lowest pair of primary leaflets 1/4–2/3 as long as the leaf blade, sessile, or on petiolules to 15 mm long, the ultimate segments 2–20 mm long, linear or narrowly elliptic; peduncles 1–9 per plant, (4) 9–28 cm long, rather densely hirtellous just below the umbel; involucre lacking, or rarely of 1 or 2 small bracts; rays (5) 9–18, 0.8–2.5 cm long, glabrous, scabrous or hirtellous; bractlets of the involucels 5–11, to 5.5 mm long, linear or narrowly elliptic, separate or united at the very base, green or sometimes with a scarious or purplish margin; pedicels obsolete or to 2 mm long; calyx teeth less than 0.5 mm long, deciduous; petals and stamens bright yellow when fresh, pale or purplish in age; styles about 2 mm long; carpophore apparently lacking to well developed and divided to the base; fruit mostly 3–6 mm long, the wings ca 1.5 mm wide, some of the dorsal ones sometimes obsolete. Grass-forb, aspen, Douglas fir, and spruce-fir communities, and windswept ridges and raw escarpments especially in limestone, at 2,375 to 3,600 m in Beaver, Emery, Garfield, Grand, Iron, Piute, San Juan, Sanpete, Sevier, Washington, and Wayne counties; southeastern Wyoming to Arizona and Durango, Mexico; 138 (vii). Occasional specimens have been confused with *Lomatium juniperinum*. The following key should aid in separating the two.

1. Peduncles hirtellous just below the umbel; rays 0.8–2 cm long, sometimes scabrous; plants otherwise glabrous, of Sanpete County and southward; petals yellow when fresh, but turning whitish in herbarium specimens; pedicels obsolete or to 2 mm long; lowest pair of primary petiolules to 1.5 cm long .... *Cymopterus lemmonii*

— Peduncles glabrous or not any more pubescent than the rest of the plant; rays 1–8 cm long; plants rarely with glabrous herbage, and then with cream or white petals, from Sanpete County and northward; pedicels 3–16 mm long; lowest pair of primary petiolules 1–3 cm long ..... *Lomatium juniperinum*

***Cymopterus longipes* Wats.** Long-stalk Spring-parsley [*Peucedanum lapidosum* Jones, type from Echo, Summit County; *C. lapidosus* (Jones) Jones; *Lomatium lapidosum* (*Jones*) Garrett]. Plants 7–30 (50) cm tall, glabrous, not aromatic, from a thickened fibrous taproot with a simple or sparingly branched crown; pseudoscapes 1–3, 4–24 cm long, mostly aerial, rarely a small portion of it subterranean, more or less enveloped by dilated bladeless sheaths; leaves whorled atop the pseudoscape, rarely any rising from the fibrous root, (1) 2 (3) times pinnately compound, with mostly 4–6 opposite or offset pairs of lateral primary leaflets, the upper pairs often more or less confluent and merely pinnatifid, petioles 1–5 cm long, blades 3–8.5 cm long, oblong to ovate in outline, the confluent portions 2–12 mm wide; lowest pair of primary leaflets 1–5 cm long, sessile, or on petiolules to 5 mm long, the ultimate lobes or teeth about 1–5 mm long, about 0.5–3 mm wide; peduncles 3–18 per pseudoscape, 4–24 cm long; umbels sometimes nodding, on the sometimes recurved peduncles; involucre lacking; rays 4–11, 0.5–3.3 cm long; bractlets of the involucel to 7 mm long, mostly less than 1 mm wide, mostly separate, green with very narrow scarious margins; pedicels 1–12 mm long; calyx teeth 0.2–0.5 mm long; petals yellow or white when fresh, when yellow fading to white in herbarium specimens; stamens the color of the petals; styles about 2 mm long; carpophore divided to the base; body of the fruit 4–6 mm long, the wings 5–8 mm long, 1–2 mm wide. Mostly in sagebrush-grass communities, but also in pinyon-juniper and mountain brush communities at 1,340 to 3,155 m in Box Elder, Cache, Carbon, Daggett, Davis, Duchesne, Juab, Morgan, Rich, Salt Lake, Sanpete, Summit, Tooele, Uintah, Utah, Wasatch, and Weber counties; southeastern Idaho and northcentral Utah to northwestern Colorado; 160 (xxi). White-flowered specimens are common in the Bear River Range and occasional to the central part of the Wasatch Range. The yellow petals of more southern specimens turn whitish in the herbarium, and the ranges of the two color variants are difficult to determine from herbarium specimens. Other than the color difference, there seems to be no way to tell the phases apart. A third phase, in which the fruits are *Lomatium*-like (dorsal ribs not or scarsely winged), apparently has white flowers. This phase, known from Summit County and adjacent Wyoming, is referable to *C. lapidosum* (Jones) Jones, which may be worthy of the specific status given it by Jones.

***Cymopterus minimus* (Mathias) Mathias** Least Spring-parsley. [*Aulospermum minimum* Mathias]. Plants 3–10 (10) cm tall, acaulescent, scabrous, from a slender to much enlarged often deep-seated taproot, with few to several often soboliferous branches; stems mostly subterranean and etiolated; pseudoscapes lacking or short and subterranean; leaves mostly 2–3 times pinnately dissected, with 3–4 opposite pairs of lateral primary leaflets, petioles 0.5–2 cm long or sometimes much longer with etiolated subterranean portions, blades 1–3 cm long, the confluent portions 1–6 (10) mm wide, the primary leaflets sessile or the lowest pair on petiolules to 0.5 cm long, the ultimate segments to 3 mm long, to ca 2 mm wide; peduncles 1.5–14 cm long; rays of the umbel mostly 5–10, 0.2–1.8 cm long; bractlets of the involucel about 3–4, 2–4 mm wide; pedicels nearly obsolete or to 3 mm long; calyx teeth minute or lacking; petals cream-pink or pale purple (reputedly white) with whitish margins or with moderately purple markings in herbarium specimens; stamens whitish; styles about 2 mm long; carpophore divided to the base; fruit 4–8 mm long, the wings to 1 mm wide. Ponderosa pine, bristlecone pine, spruce-fir, and perhaps pinyon-juniper communities, at (2,190) 2,440 to 3,170 m, in Garfield, Iron, and Kane counties; endemic; 23 (i). Occasional specimens are intermediate to *C. purpureus*, and more work is needed to establish the range of the small plants with cream-pink or pale purple petals. These plants have been confused with *C. purpureus* var. *rosei*, and they are similar in the short rays, short pedicels, small fruit, small leaves, and scabrosity, but the leaves are not ternate, and they are more finely dissected than those of *C. purpureus* var. *rosei*. In some features of the leaves and in distribution this taxon is more closely allied with *C. purpureus* var. *purpureus*. At the extreme (Cedar Breaks) these plants are very different, but through a series of recent collections from the Markagunt, Paunsaugunt, and Table Cliff plateaus and Escalante Mountains, a rather close relationship to *C. purpureus* var. *purpureus* is evident. Perhaps this is only a part of the *C. purpureus* complex and could be treated as a variety, but no such combination is proposed herein. The color of the petals seems to be diagnostic.

***Cymopterus multinervatus* (Coult. & Rose) Tidestr.** Purple-nerved Spring-parsley. [*Phellopterus multinervatus* Coult. & Rose]. Plants 10–15 cm tall, glabrous and glaucous, from a linear or slightly to much enlarged fibrous taproot; pseudoscapes lacking or solitary, to 7.5 cm long, partly or mostly subterranean, often enveloped by dilated, scarious bladeless sheaths; leaves basal or whorled, with the peduncles atop the pseudoscape, 2–3 times pinnately compound, with 3–5 opposite pairs of lateral primary leaflets; petioles 1–7.5 cm long; blades 1–7 cm long, ovate in outline, lowest pair of primary leaflets to 4.5 cm long, sessile or on petiolules to 5 mm long, the ultimate lobes to 4 (7) mm long, to 2 mm wide, sometimes with small rounded teeth; peduncles 1–8, 4–10 cm long; involucre to 1 (1.5) cm long, the bracts more or less united, sometimes forming a cup or reduced to a ring, greenish basally and centrally, with broad, white scarious margins, multinerved, the nerves purplish, more or less parallel; rays (3) 5–11, 0.3–1 cm long, obscured by the dense fruits, included in or exserted beyond the involucre; involucels 5–10 mm long, like the involucre in color, texture, and venation, but never reduced to a ring; pedicels to about 4 mm long, included in the involucel; calyx teeth 0.5–1 mm long or somewhat enlarged and simulating the involucre; petals white or purple; stamens white or purple; styles about 2–3 (4) mm long; carpophore lacking; body of the fruit 7–10 mm long, the wings 12–13 mm long, 5–7 mm wide. Desert shrub and sagebrush communities at 1,220 to 1,525 m in Kane and Washington counties; southern Utah to southern California and to southwestern Texas and northern Mexico; 7 (0).

***Cymopterus newberryi* (Wats.) Jones** Sweetroot Spring-parsley. [*Peucedanum newberryi* Wats.]. Plants 7–18 cm tall, more or less slighty viscid and often dotted with adhering sand grains, from a slender or slightly to much enlarged fibrous taproot with simple or rarely branched crown; pseudoscape lacking; leaves arising directly from the fibrous root, ternate, rarely simple and ternately cleft; petioles 3.5–10.5 cm long, (1.6) 2.5–5 times as long as the blades, often partly subterranean, blades 1–4(5.5) cm long, confluent portions 5–35 mm wide; leaflets 1–3.5 cm long, cleft or divided and mostly ternately so, the major lobes again lobed or toothed and often ternately so, the ultimate lobes or teeth to 6 mm long, to 5 mm wide; peduncles 1–10, 5–17 cm long, often partly subterranean; involucre lacking; rays 5–16, the central ones often greatly reduced or obsolete, the outer ones 1–3.3 cm long; bractlets of the involucels 3–12 mm long, to 3 mm wide, entire, green, or sometimes purplish in age, with texture of the leaves; pedicels about 1 mm long; calyx teeth about 0.5 mm long, deciduous; petals and stamens yellow when fresh, fading to cream or greenish cream in herbarium specimens; styles about 2–3 mm long; carpophore lacking; body of fruit 5–8 mm long, the wings 6–10 mm long and 1–1.5 mm wide, more or less corky, some of the dorsal ones obsolete. Desert shrub, blackbrush, sand sagebrush, desert grassland, and juniper communities, mostly on very sandy soil, at 850 to 1,830 m in Beaver, Garfield, Grand, Kane, Millard, San Juan, Washington, and Wayne counties; southern Utah and northern Arizona; 47 (x).

Cymopterus purpurascens **(Gray) Jones** Widewing Spring-parsley [*C. montanum* var. *purpurascens* Gray]. Plants 5–15 cm tall, glabrous and glaucous, from a mostly enlarged tuberlike fibrous taproot with simple or sparingly branched crown, the crown usually with few to several persistent shredded leaf bases; pseudoscapes lacking or to 3 per plant and to 6 cm long, mostly subterranean, usually enveloped by scarious dilated bladeless sheaths; leaves basal or more or less whorled atop the pseudoscape, 2–3 times pinnately compound, with 3–6 opposite pairs of lateral primary leaflets, the pairs gradually reduced upward, petioles 0.6–5 cm long, sometimes longer including etiolated subterranean portions, blades 1.2–7 cm long, oblong to ovate in outline, confluent portions to 3 (5) mm wide, lowest pair of primary leaflets (0.4) 1–2 (4) cm long, sessile or on petiolules to 3 mm long, the ultimate lobes or teeth rounded, mostly with narrow-scarious margins; peduncles 1–3 per pseudoscape, 3–9 cm long; involucre 8–14 mm long, more or less united at the base and sometimes to about midlength, whitish, scarious, the lobes with a greenish or purplish midnerve extending to the tip, and usually 1 or 2 parallel lateral, much shorter nerves; rays about 4–7, rarely longer than 1 cm, mostly shorter than the involucre, hidden in the dense broadly winged fruits; involucels like the involucre but shorter (about 5–7 mm) and usually with the lateral nerves over 1/2 as long as the midnerve, the nerves occasionally branched; pedicels to 5 mm long, mostly concealed in the involucels and in the dense fruits; calyx teeth less than 0.5 mm long, rounded; petals white or purplish with a green or purplish midvein; filaments white, anthers purple; styles about 2 mm long; carpophore lacking or hairlike and less than 0.02 mm wide, not persisting on the pedicel; body of fruit 6–11 mm long, the wings 9–16 mm long and 3–6.5 mm wide. Desert shrub, sagebrush, pinyon-juniper, bullgrass, and ponderosa pine communities, on aeolian sand to heavy clay at 1,065 to 2,745 m in all Utah counties except Daggett, Davis, Grand, Morgan, Rich, Summit, Wasatch, and Weber; southeastern Idaho to southeastern California and northwestern New Mexico; 106 (xxi). *Cymopterus purpurascens* is often confused with *C. bulbosus*, but it is distinguished by a number of features. In addition to those listed in the key, the lobes of the involucre and involucel of *C. bulbosus* mostly are only 1-nerved, this occasionally with 1 or 2 short lateral nerves. The involucre is sometimes reduced to a ring or cup in *C. bulbosus*, but it is always well developed in *C. purpurascens*; *C. bulbosus* also flowers later (often a month or so) than does *C. purpurascens*, and it is confined to lowlands mostly of heavy soil, whereas *C. purpurascens* is found on a wide range of sites and soils. However, rare specimens (Neese 7169 and Thorne et al. 1707) show the broad wings of fruit typical of *C. purpurascens*, but they have rays well over 1 cm long that are exserted beyond the involucre, and at least some of the fruits have a well-developed carpophore. Perhaps these specimens indicate rare hybridization of these two taxa.

Cymopterus purpureus **Wats.** Variable Spring-parsley. Plants 5–26 cm tall, from a slender to much thickened fibrous taproot with a simple or branched crown; stems solitary to several, arising at or just below ground level; pseudoscape mostly lacking, mostly less than 2 cm long when present and then usually mostly subterranean; leaves basal or nearly so, ternate or (1) 2–3 times pinnately compound, with up to 4 opposite pairs of lateral primary leaflets, petioles 1–7 cm long, blades 1.5–13 cm long, mostly ovate in outline, lowest pair of primary leaflets mostly over 1/2 and to 3/4 as long as the leaf blade, sessile or on petiolules to 32 mm long, the ultimate lobes or teeth acute or rounded; peduncles 1–5, 3–21 cm long; involucre lacking; rays 5–22, 0.2–9.5 cm long; bractlets of the involucel 4–8, 2–4 mm long, separate or united at the base, acute to acuminate, entire; pedicels 1–10 mm long; calyx teeth less than 0.5 mm long, deciduous; petals yellow when fresh, drying dark purple in the field or within a year or 2 in herbarium specimens; stamens yellow when fresh, remaining yellowish or cream or at least pale in herbarium specimens; styles about 2–3 mm long; carpophore divided to the base; body of the fruit about 4–8 mm long, the wings 5–10 (12) mm long, 1.5–4 mm wide, often marked with purple. With 3 more or less integrading varieties in the state.

1. Fruiting rays 5–8 (15), 0.2–2 (3) cm long; fruiting pedicels 1–5 (7) mm long; wings of fruit 5–8 mm long, to 2 mm wide; leaf blades 1–3.5 (4) cm long, mostly (not always) ternate, the leaflets with rounded lobes; plants glabrous, or more often scabrous, lower to midmontane, mostly of central Utah . . . . *C. purpureus* var. *rosei*

— Fruiting rays (8) 12–22, (2) 2.5–7 (9.5) cm long; fruiting pedicels 5–10 mm long; wings of fruit 8–10 (12) mm long, (2) 2.5–4 mm wide; leaf blades commonly 3–9 (13) cm long, pinnately compound, rarely ternate, often with acute ultimate segments, plants mostly glabrous, rarely scabrous, of deserts and lower montane, widespread 2

2(1). Plants conspicuously glaucous, of Washington, Iron, and Beaver counties; some wings of fruit apparently thickened and spongy; ultimate teeth of leaves acute . . . . *C. purpureus* var. *jonesii*

— Plants not conspicuously glaucous, not of the above counties except Washington; wings of fruit mostly thin and papery; ultimate teeth of leaves acute to rounded . . . . *C. purpureus* var. *purpureus*

Var. *jonesii* (Coult. & Rose) Goodrich, comb. nov. [based on: *Cymopterus jonesii* Coult. & Rose Rev. N. Amer. Umbell. 80. 1888; *Aulospermum jonesii* (Coult. & Rose) Coult. & Rose]. Sagebrush, pinyon-juniper, and mountain brush communities at 1,520 to 1,905 m in Beaver, Iron, and Washington counties; southwestern Utah and adjacent Nevada; 10 (i).

Var. *purpureus* Desert shrub, sagebrush, pinyon-juniper, mountain brush, ponderosa pine, and rarely aspen-fir communities in sandy to heavy clay soils at 1,100 to 2,375 (2,880) m in Carbon, Duchesne, Emery, Garfield, Grand, Kane, San Juan, Uintah, Washington, and Wayne counties; eastern and southern Utah, western Colorado, northern Arizona, and northwestern New Mexico; 134 (v). Specimens with rather broad leaflets from the Uinta Basin (Neese et al. 7273, and White and Neese 123) indicate a close relationship to and possible hybridization with *C. duchesnensis*.

Var. *rosei* (Jones) Goodrich, comb. nov. [based on: *Aulospermum rosei* Jones in Coult. & Rose. Contr. U.S. Nat. Herb. 7: 179. 1900; *C. rosei* (Jones) Jones]. Pinyon-juniper, sagebrush, mountain brush, bull grass, limber pine, white fir, and rarely desert shrub communities, in marly limestone, shaley slopes, and clay or sandy clay soils at (1,615) 1,760 to 2,290 (2,650) m in Duchesne, Juab, Millard, Sanpete, Sevier, and Wasatch counties; endemic to central Utah; 28 (x). The plants from the Sevier drainage are quite removed from plants of the rest of the complex. In this case the differences seem to be a function of isolation, but the Duchesne County materials are not so isolated from plants of var. *purpureus*. The differences in this case seem to be more a function of ecological stress than of isolation. An independent origin is suggested. Random plants of var. *purpureus* with features intermediate to those of var. *rosei* are found in other parts of the range of var. *purpureus* (Neese 5775; Foster 4380, 8338; and N. H. Holmgren et al. 1998). Most of the plants of the Sevier drainage are quite different from those of var. *purpureus*, but some would be difficult to place without location data (Welsh 12803; Neese & White 2925; and anonymous 1322a, UT 11951). Recognition at varital level seems appropriate.

***Cymopterus terebinthinus* (Hook.) T. & G.** Rock Parsley. [*Selinum terebinthinum* Hook.; (*Pteryxia terebinthina* (Hook.) Coult. & Rose]. Plants (12) 15–35 (40) cm tall, glabrous, strongly aromatic, from a heavy, nearly woody root surmounted by a mostly branched caudex, the caudex clothed with leaf bases that often persist for a few years without shredding; pseudoscape lacking; leaves basal and often 1–3 on the lower 1/3 (1/2) of the stem, mostly 2–4 times pinnately or ternate-pinnnately compound, with (4) 6–10 opposite or offset pairs of lateral primary leaflets, petioles 2–13 cm long, blades 1.5–14 cm long, finely and completely dissected so that the ultimate segments are the widest undivided part of the blade, lowest pair of primary leaflets mostly 3–9 cm long, (1/5) 1/2–3/4 as long as the leaf blade, on petiolules 2–4 cm long, the ultimate segments 1–5 (7) mm long, 0.5–1 (1.5) mm wide; peduncles 10–34 cm long; involucre lacking; rays 7–13, 0.7–5 (8) cm long; bractlets of the involucel (0) 1–5, 2–5 mm long, separate or united at the base, linear or linear-subulate; pedicels 2–5(10) mm long; calyx teeth 0.5–0.9 mm long, acute, rather persistent; petals and stamens bright yellow when fresh, fading whitish and rarely yellow for more than 2 years in herbarium specimens; fruiting styles (2–5) 3–4 mm long, mostly curved or coiled; carpophore divided to the base, persisting on the pedicel; body of fruit 5–8 mm long, the wings 6–9 mm long, 0.5–1.5 (2.5) mm wide, some of the dorsal ones sometimes reduced or obsolete. There are two varieties in Utah.

1. Lateral pairs of primary leaflets all longer than their internodes; lowest pair of primary leaflets various but often less than 4 times as long as wide, with the lower secondary leaflets sometimes petiolulate; leaf blades not skeletonlike, the ultimate segments appearing to be more numerous or longer or both than in the following variety; plants of the Uinta Basin and northern Utah. . . . . *C. terebinthinus* var. *calcareus*

— Upper 4–6 pairs of lateral primary leaflets equal or shorter than their internodes; lowest pair of primary leaflets 4–10 times longer than wide, with sessile secondary leaflets; leaf blades skeletonlike, the ultimate segments appearing to be fewer or shorter or both than in the preceding variety; plants of eastern Utah south of the Uinta Basin . . . . *C. terebinthinus* var. *petraeus*

Var. *calcareus* (Jones) Cronq. [*Cymopterus calcareus* Jones]. Desert shrub, sagebrush, pinyon-juniper, and mountain brush communities, often in talus, colluvium, and crevices of rock outcrops at 1,445 to 2,320 (2,560) m in Box Elder, Cache, Daggett, Juab, Rich, and Uintah counties; Montana to Colorado, and west to southern Idaho and northeastern Nevada; 36 (vii). Some of the Uintah County materials are transitional to plants of var. *petraeus*. Plants of var. *calcareus* are very similar to those of *C. terebinthinus* var. *albiflorus* (T. & G.) Jones, which was originally described as having white flowers. Dried flowers soon turn white or whitish in all of the *C. terebinthinus* complex, and the two varieties are both reported from the same regions of Montana and Wyoming. Unfortunately, the misnomer var. *albiflorus* has priority by many years, and our plants might belong to that taxon.

Var. *petraeus* (Jones) Goodrich, comb. nov. [based on: *C. petraeus* Jones Contr. W. Bot. 8: 32. 1898]. Skeletonleaf Rock-parsley. Desert shrub, blackbrush, and pinyon-juniper communities, often in talus, colluvium, crevices of rock outcrops, and in sandy to clayey soil at 1,400 to 2,075 m in Emery, Grand, and San Juan counties; Great Basin in Nevada and southern Idaho, and Colorado drainage in Utah and northwestern Arizona; 16 (i). The disjunction from the Great Basin in Nevada to the Colorado Basin in Utah without occurrence in the Great Basin in Utah is most unusual. An independent origin is suggested for the Utah materials, which at present are known to be separated from plants of var. *calcareus* only by Desolation Canyon of the Green River. The Colorado drainage materials are as skeletonlike or more so than the Nevada materials but are not so distinct as to warrant separate status, even if from an independent origin. Neither the Nevada nor Utah materials are so distinct from plants of var. *calcareus* as to warrant recognization at the species level. They fit well into *C. terebinthinus* both morphologically and in volatile oils, and they are surrounded on 3 sides by other varieties of *C. terebinthinus*. Without distribution data some of the San Juan County specimens as well as some from central Nevada would be nearly if not wholly impossible to distinguish from some specimens of var. *calcareus* of the Uinta Basin.

Daucus L.

Annual or biennial caulescent herbs from taproots; leaves pinnately dissected; umbels compound; involucre of pinnatifid bracts or lacking; involucel of toothed or entire bracts or lacking; calyx teeth evident to obsolete; petals white or those of the central flower of the umbel or umbellet often purple or rarely all the flowers pink or yellow; stylopodium conic; carpophore entire or bifid at the apex; fruit oblong to ovoid, slightly compressed dorsally, evidently ribbed dorsally, with two ribs on the commissure, beset with stout spreading glochidiate or barbed ribs.

1. Plants biennial, introduced, cultivated and occasionally escaping and then somewhat weedy; widespread; bracts of the involucre mostly pinnatifid into mostly entire rather rigid elongate segments . . . . *D. carota*

— Plants annual, native, not cultivated, known from the Virgin Narrows in Arizona, to be expected in Washington County; bracts of the involucre pinnatifid into often lobed or toothed nonrigid segments . . *D. pusillus* Michx.

Daucus carota **L.** Carrot. Plants 6–10 dm tall, from a taproot; herbage glabrous or hirsute; leaves in rosettes and cauline, mostly 1–2 times pinnate and then pinnatifid, with about 4–9 opposite or offset pairs of lateral primary leaflets, basal and lower cauline petioles to 15 cm long, basal and lower blades 5–15 cm long or more, the upper ones reduced and sessile on dilated sheaths, lowest pair of primary leaflets about 1/3–1/2 as long as the leaf blade, on petiolules 4–15 mm long, ultimate segments 1–10 mm long, 0.5–2 mm wide, elliptic, or narrowly deltoid, or linear, often acute; peduncles mostly 8–30 cm long; umbels 4–10 or more; involucre of pinnatifid bracts 1–5 cm long, the segments linear and narrow; rays about 15–60 or more, (0.5) 1–6 cm long; involucels similar to the involucre but smaller, or the bractlets entire, 2–16 mm long; fruit 3–4 mm long, bristly hirsute in rows, the hairs or bristles about 2 mm long, minutely glochidate at the apex, the intervals often with shorter simple hairs. Cultivated in all counties of the state, wild (mostly along ditchbanks and waste places) mostly in the more populated counties of the state; introduced from Eurasia; 16 (iv). The wild plants (ssp. *carota*) differ from the cultivated plants [ssp. *sativus* (Hoffm.) Arcangeli] primarily in the size and flavor of the root.

Foeniculum Adans.

Biennial or perennial, caulescent herbs with strong odor of anise, glabrous, glaucous, from a taproot; leaves pinnately dissected with filiform ultimate segments; umbels compouund; involucre and involucel lacking; calyx teeth obsolete; petals yellow; stylopodium conic; carpophore divided to the base; fruit oblong, subterete, or slightly compressed laterally, with prominent ribs.

Foeniculum vulgare **Mill.** Sweet Fennel. Short-lived perennial herbs 1–2 m tall, from a taproot; stems solitary, branched above; leaves to 3-times ternate-pinnately compound with about 6–9 opposite pairs of ateral primary leaflets; petioles to about 15 cm long rather abruptly expanded into a dilated sheathing base or lacking and blades arising directly from the sheath; larger blades to 30 or 40 cm long, ovate in outline, finely and completely dissected, the elongated filiform ultimate segments 4–40 mm long and less than 1 mm wide, the lowest pair of primary leaflets on petiolules often over 2 cm long; peduncles 1.5–6.5 cm long; umbels several; rays 10–40, 2–8 cm long; petals yellow; styles 0.3–0.4 mm long; fruit 3.5–4 mm long. Roadsides and waste places at 850 to 1,465 m in Utah and Washington counties; native of the Mediterranean region, widely introduced elsewhere, and in much of the United States especially toward the south, perhaps not well adapted to much of Utah except Washington County; 3 (0).

Heracleum L.

Biennial or perennial herbs from a taproot or fascicle of fibrous roots, leaves ternately or pinnately compound, with broad toothed or cleft leaflets; umbels compound; involucre lacking or of a few deciduous bracts; involucel lacking or of slender bractlets; flowers of the marginal umbellets generally irregular, the outer petals enlarged and often deeply bilobed; calyx teeth obsolete or minute; stylopodium conic; carpophore divided to the base; fruit orbicular to obovate or elliptic, strongly flattened dorsally, usually pubescent, the dorsal ribs narrow, the lateral ribs broadly winged.

BRUMMIT, R. K. 1971. Relationship of *Heracleum lanatum* Michx. of North America to *H. sphondylium* of Europe. Rhodora 73:578–584.

Heracleum lanatum **Michx.** Cow parsnip. [*H. sphondylium* ssp. *lanatum* (Michx.) A. & D. Love]. Stout single-stemmed perennial herbs 8–25 dm tall, from a taproot or cluster of fibrous roots, glabrate or thinly to densely villous or villous-hirsute below to villous-woolly above, especially on the nodes; leaves ternate or the upper ones simple, petioles to 25 cm long or longer, or lacking on upper leaves with the petiolules and rachis arising directly from a dilated sheath, blades to 40 cm long or longer, ovate to orbicular; leaflets 8–36 cm long or longer, ovate to orbicular, usually with 3 major lobes that are again lobed and coarsely toothed; peduncles 5–24 cm long; involucre lacking or of few mostly linear entire bracts to 2 cm long; rays 12–25, 3.5–12 cm long; involucels of 3–5 linear, subulate or caudate bractlets to 15 mm long; pedicels 6–26 mm long; petals white (2) 4–8.5 mm long, at least some deeply bilobed; filaments white, anthers whitish to dark green or yellow with pollen; styles about 1 mm long, the stigmas incurved; fruit 8–12 mm long, obovate to obcordate, strongly flattened, the lateral ribs with wings about 1–1.5 mm wide, the dorsal ribs filiform. Aspen, tall forb, fir, oak-maple, willow, streamside, and wet meadow communities and around seeps and springs at 1,430 to 2,930 m in Box Elder, Cache, Carbon, Davis, Duchesne, Juab, Salt Lake, Sanpete, Sevier, Summit, Tooele, Uintah, Utah, Wasatch, and Weber counties; Eurasia and across much of North America; 61 (iii).

Hydrocotyle L.

Perennial herbs; stems creeping or floating, rooting at the nodes; leaves petiolate, often peltate; inflorescences sessile, or borne on axillary peduncles; involucres small or lacking; petals white, greenish, or yellow; calyx minute or lacking; stylopodium conic to depressed; fruit orbicular to ellipsoid, more or less flattened laterally, the dorsal surfaces rounded or acute, the ribs obsolete or narrow and acute; carpophore lacking.

Hydrocotyle verticillata **Thunb.** Water Pennywort. Plants glabrous, with slender creeping stems; leaves peltate, suborbicular, 0.5–6 cm wide, shallowly lobed and often crenate; petioles slender, 3–20 cm long or longer; peduncles slender, axillary; flowers apparently verticillate in few to several well-separated whorls; petals pale, small; fruits subsessile, subtruncate at the base, 1.5–2 mm long, 2–3 mm wide. Moist ground or in water at 850 to 1,005 m in Washington County; South America north to Massachussetts and California; 4 (0).

Ligusticum L.

Perennial caulescent or acaulescent herbs from taproots; leaves ternately or ternate-pinnately compound or dissected, the lower ones with well-developed petioles, the upper ones with blades arising directly from dilated sheaths; umbels compound; involucre and involucel lacking or of a few narrow bracts or bractlets; calyx teeth evident or obscure; petals white; stamens white; stylopodium low-conic; carpophore divided to the base; fruit oblong to ovate or suborbicular, subterete or slightly compressed laterally, the ribs evident, often winged.

1. Ultimate leaf segments more or less linear or very narrowly elliptic, mostly 0.5–3 mm wide, entire 2

— Ultimate leaf segments (at least some) elliptic or broader, some usually over 3 mm wide, sometimes toothed or lobed 3

2(1). Umbels mostly solitary, occasionally 2, rarely 3, never opposite; rays 0.5–3.6 cm long; petioles 1.2–13.5 cm long; leaf blades 3–19 cm long; plants 10–45 (64) cm tall, of the Uinta Mountains . . . . *L. tenuifolium*

— Umbels 2–5 or more, the lateral ones occasionally opposite or whorled; rays 2.5–6.5 (8) cm long; petioles 8–32 cm long; leaf blades (9) 12–30 cm long; plants (40) 60–100 cm tall, of central Utah and western Uinta Mountains . . . . *L. filicinum*

3(1). Umbels 2 or 3, the lateral 1 or 2 alternate, subtended by much reduced leaves; plants of the Raft River Mountains . . . . *L. grayi*

— Terminal umbel subtended by often opposite or whorled umbels and 1–3 or more alternate umbels from the axils of reduced or well developed leaves; plants widespread . . . *L. porteri*

Ligusticum filicinum **Wats.** Fernleaf Ligusticum. Plants (4.5) 6–13 dm tall, aromatic, glabrous, from a heavy taproot with a simple or branched crown, the crown clothed with fibrous persisting petiole bases; leaves basal and 1–3 cauline, ternate-pinnately 3 times dissected, with 5–6 (7) opposite pairs of lateral primary leaflets, basal petioles 8–32 cm long, blades (9) 12–30 cm long, ovate in outline, lowest pair of primary leaflets 1/2–3/4 as long as the leaf blade, on petiolules 2.5–10 cm long; ultimate leaf segments 1–18 mm long, 0.75–2.5 (3) mm wide, linear, very narrowly elliptic or narrowly deltoid, entire or bifid or trifid; peduncles (5) 10–17 (23) cm long; terminal umbel subtended by 1–3 smaller umbels, the lateral ones arising from axils of leaves and alternate or the upper ones not from leaf axils and opposite or rarely 3 per node; involucre lacking; rays 7–27, 2.5–6.5 (8) cm long; involucels of 1–3 linear separate usually deciduous bractlets to 5 mm long; pedicels 4–12 mm long; petals white; stamens whitish; styles ca 0.5 mm long; fruit 5–8 mm long. Tall forb, aspen, sagebrush-grass, forb-grass, Douglas fir, and spruce-fir communities at (1,920) 2,377 to 3,110 m in Cache, Duchesne, Juab, Morgan, Sanpete, Summit, Tooele, Utah, and Wasatch counties; Idaho, Montana, Utah and Wyoming; 46 (xx). This taxon is rather easily confused with *L. porteri* (q.v).

***Ligusticum grayi* Coult. & Rose** Grays Ligusticum. Plants 3–6 (9.5) dm tall, glabrous, aromatic, from a stout taproot with simple or branched crown, the crown clothed with fibrous persisting petiole bases; leaves basal and usually 1–3 much reduced cauline ones, ternate-pinnately twice compound and then pinnatifid with (2) 3–5 opposite pairs of lateral primary leaflets, petioles (2.5) 4–34 cm long, blades 4–26 cm long, ovate in outline, lowest pair of primary leaflets 1/2–3/4 as long as the blade, on petiolules 1–6.5 cm long, the larger secondary leaflets pinnatifid with the larger lobes again bilobate or trilobate; peduncles 2–55 (90) cm long; terminal umbel subtended by 1–2 alternate umbels arising from the axils of much reduced leaves; involucre lacking or rarely of 1 linear mostly deciduous bract to about 1 cm long; rays 8–18, 1.2–4 cm long; involucels lacking or of 1–5 linear bractlets to 4.5 mm long; pedicels 4–10 mm long; petals white; stamens whitish; styles 0.8–1.1 mm long; fruit 4–6 mm long. Forb-grass and fir communities and snowflush areas at 2,650 to 2,900 m in the Raft River Mountains, Box Elder County; Washington to California and east to Idaho and northwestern Utah; 3 (iii).

***Ligusticum porteri* Coult. & Rose** Southern Ligusticum. [*L. brevilobum* Rydb., type from the Aquarius Plateau]. Similar to L. filicinum, but leaves with broader ultimate segments, these (1.5) 3–8 mm wide, and with the terminal umbel often subtended by a whorl of 3–8 lateral umbels, and occasionally with up to 12 or more umbels, but sometimes with the lateral umbels only 2 and opposite, but not alternate. Sagebrush, oak, aspen, Douglas-fir, spruce, fir, and occasionally in open forb-grass communities at 2,255 to 3,171 m in Beaver, Carbon, Duchesne, Garfield, Grand, Iron, Juab, Kane, Millard, Piute, San Juan, Sanpete, Sevier, Uintah, and Utah counties; southern Wyoming to northern Mexico, west to Idaho and Arizona; 58 (x). Plants of this taxon are sometimes mistaken for *Conioselinum scopulorum* (q.v.). The separation of *L. porteri* from *L. filicinum* is made difficult by a rather extensive overlap in distribution and lack of definitive morphology from Utah County south to Sevier County. Otherwise the ranges of the two taxa are essentially discrete in Utah, but occasional specimens from scattered locations throughout the state would be difficult to place without location data.

***Ligusticum tenuifolium* Wats.** Small Ligusticum; Slender-leaf Ligusticum. [*L. filicinum* var. *tenuifolium* (Wats.) Mathias & Const.]. Plants 11–64 cm tall, glabrous mildly aromatic from a taproot, the crown more or less covered by short shredded old leaf bases; leaves basal and sometimes 1 or 2 cauline, ternate and then 2–3 times pinnate with 5–7 pairs of lateral primary leaflets; petioles 1.2–13.5 cm long; blades 3–19 cm long, completely dissected, ovate in outline; lowest pair of primary leaflets about 1/2 to 2/3 as long as the blade, on petiolules (0.5) 1–4 cm long, the upper primary leaflets progressively reduced, the ultimate segments 2–9 mm long, 0.5–1.5 (2.5) mm wide; scapes or peduncles 10–45 (61) cm long; involucre lacking; umbel solitary or the terminal one sometimes subtended by a lateral 1 (very rarely 2) that usually arises from the axil of a reduced leaf; rays 6–15, 0.5–3.6 cm long; involucels lacking or of 1–3 filiform-linear bractlets to 3 mm long; pedicels 2–4 mm long; calyx obsolete; petals about 1 mm long, white, sometimes tinged with light purple in age; stylopodium evident, conic; styles 0.5–0.8 mm; fruit about 3–5 mm long. Moist and wet meadows, along streams in lodgepole pine and Engelmann spruce woods at 2,440 to 3,420 m, common across the Uinta Mountains, in Daggett, Duchesne, Summit, Uintah, and Wasatch counties; northeast Oregon to western Montana south to Colorado and Uinta Mountains of Utah; 37 (xviii). Through a series of features (none of which are exclusive), plants of *L. tenuifolium* are readily distinguished from those of *L. filicinum*. The two taxa are sympatric in the western Uinta Mountains, where somewhat intermediate specimens occur, but the range of overlap is small and few specimens seem intermediate.

Lomatium Raf.

Plants perennial, acaulescent or caulescent, occasionally with a short pseudoscape, glabrous or pubescent, from a slender tap root that sometimes has 1 or more tuberlike segments, or from a thickened, woody branching caudex, sometimes clothed at the base with marcescent material; stems simple or rarely branched and thus peduncles and umbels mostly solitary; leaves pinnate or pinnately to ternate-pinnately compound, sheaths often dilated especially in lower leaves, petioles well developed and distinct or confluent with and poorly differentiated from the sheath, or lacking and the petiolules arising directly from the sheath, ultimate segments extremely variable; involucre lacking or inconspicuous; rays few to many, spreading to ascending, the central ones often shorter and sterile; involucel mostly of separate or partly united bractlets, rarely lacking; pedicels slender or stout, the central ones often shorter and sterile; petals small, yellow, white, greenish yellow or purplish; calyx teeth obsolete or small, or conspicuous in a very few species; styles slender, often curved or coiled; stylopodium lacking; carpophore divided to the base; fruit linear to orbicular or obovate, flattened dorsally, glabrous or pubescent, dorsal ribs filiform or obsolete or occasionally with rudimentary wings at base. **Note:** The genus is closely related to the genus *Cymopterus*, and the filiform, wingless, dorsal ribs of the fruit seem the only consistent difference from *Cymopterus*. The dependability of this separation is somewhat weakened by the tendency for lack of dorsal wings in some taxa of *Cymopterus*.

1. Leaves once-pinnate and/or the ultimate segments over 15 mm long and less than 50 per leaf; plants glabrous and/or petals yellow when fresh 2

— Leaves more than once-compound, the ultimate segments not over 15 mm long and mostly over 50 per leaf, or if a few ultimate segments over 15 mm long or less than 50 per leaf then plants pubescent and petals white 9

2(1). Leaves once-pinnate or partly bipinnate, the leaflets sessile and more or less confluent with the rachis; plants from stout, more or less woody caudices, clothed at the base with long-persisting leaf bases, from the southern 1/2 of the state. 3

— Leaves more than once-compound, the primary leaflets mostly with well-developed petiolules, not confluent with the rachis; (plants from taproots or small caudices, not much if at all clothed at the base with long-persisting leaf-bases, from the northern 1/2 of the state except in *L. nuttallii* and then plants keyed both ways) 6

3(2). Leaflets lanceolate to elliptic, 2–12 mm wide, some always over 5 mm wide; plants of Grand and northern San Juan counties . . . *L. latilobum*

— Leaflets linear, not over 4 mm wide; distribution not as above 4

4(3). Leaves with 1–7 elongate, terete leaflets that simulate the rachis in diameter and shape, these 1–18 cm long, at least some commonly over 5 cm long in each leaf; calyx teeth greenish, acute, somewhat persistant, about 1 mm long; fruit 8–12 mm long; plants of Emery, Garfield, and eastern Sevier counties, mostly below 716 m . . . . *L. junceum*

— Leaves either with more than 7 leaflets and/or leaflets less than 5 cm long and more or less flattened and at least slightly wider than the rachis; calyx teeth not over 0.6 mm long, scarious or greenish; fruit various; distribution not as above, mostly of higher elevations 5

5(4). Plants 2–12 (17) cm tall, of Garfield and Iron counties; fruit 4–7 mm long, leaflets 3–13 per leaf, 0.2–1.5 (2) cm long . . . . *L. minimum*

— Plants 15–30 cm tall or taller, not known from the above counties; fruit 5–15 mm long; leaflets sometimes more than 13 per leaf, sometimes over 2 cm long . . . . *L. nuttallii*

6(2). Ultimate leaflets ovate to nearly orbicular or a few broadly elliptic, less than 3 times as long as wide, at least some dentate-toothed on the upper 1/4; rays (4) 8–19 cm long; peduncle often swollen just beneath the umbel; plants of the Deep Creek Mountains and western Box Elder County . . . . *L. nudicaule*

— Ultimate leaflets linear to elliptic, 3 or more times longer than wide, entire; rays 0.5–10 cm long; peduncle not swollen just beneath the umbel; distribution not as above 7

7(6). Plants caulescent, glabrous; peduncles to 13 cm long; involucel lacking; root very slender, sometimes with 1 or more globose or fusiform tuberous segments; ultimate leaflets and rays very unequal . . . . *L. ambiguum*

— Plants acaulescent or if caulescent then the peduncles mostly over 13 cm long and plants puberulent; involucels present, to 1 cm long; root not as above; ultimate leaflets and rays various 8

8(7). Plants from thickened woody branching caudices, glabrous, strongly aromatic, often of rocky places, escarpments, or semibarrens; caudex often clothed with old long-persisting leaf bases; leaves strictly basal, the ultimate leaflets 0.3–5(6.5) cm long; 0.5–2(4) mm wide; lateral wings of the fruit to 1 mm wide . . . . *L. nuttallii*

— Plants from taproots or small caudices, puberulent at least on the peduncle, not strongly aromatic, mostly growing in loamy soil; old leaf bases lacking or weakly persisting; leaves basal and sometimes 1–3 cauline, the ultimate leaflets 1–13 cm long, 1–6(15) mm wide; lateral wings of the fruit 1–2 mm wide . . . . *L. triternatum*

9(1). Larger mature leaves with blades (10) 15–30 cm long, ternate-pinnately compound, the larger ultimate segments 2–3 mm wide; plants 30–130 cm tall, peduncles fistulose, (3) 4–6 (10) mm thick at the base . . . . *L. dissectum*

— Blades of leaves 2–11 cm long or if longer then either not at all ternate or with ultimate segments not over 1 mm wide; plants rarely over 50 cm tall; peduncles fistulose or not, often less than 4 mm thick 10

10(9). Plants pubescent; petals white or yellow . . . 11

— Plants glabrous or at most scabrous; petals yellow or if white then plants keyed both ways 15

11(10). Ovaries and fruit glabrous or occasionally somewhat scabrous; plants of the central part and the northern 1/2 of eastern Utah (rare specimens of *L. nevadense* from southern Utah will key here) 12

— Ovaries and young fruit rather densely pubescent older fruit sometimes glabrous but often retaining some hirtellous hairs; plants of the central, western, and southern parts of Utah 13

12(11). Bractlets of the involucel about 10, the longer ones 4–10 mm long, pubescent; herbage more or less villous; leaves with about 4 opposite pairs of primary lateral leaflets, the lowest pair sessile or on petiolules to 1 cm long; mature fruit 9–12 (15) mm long . . . . *L. macrocarpum*

— Bractlets of the involucel 1–5, 1–4.5 mm long, glabrous; herbage glabrate to puberulent; leaf blades with (3) 4–6 opposite pairs of lateral primary leaflets, the lowest pair on petiolules 1–3 cm long; mature fruit 5–8 (11) mm long (rare specimens of *L. nevadense* with glabrous ovaries will key here, but then the primary leaflets all sessile or nearly so) . . . . *L. juniperinum*

13(11). Longer ultimate segments of leaves 5–27 mm long, some often over 1 mm wide; leaves mostly with 4 opposite pairs of sessile or nearly sessile lateral primary leaflets; root slender, usually with a deep-seated globose or fusiform tuberous segment; bractlets of the involucel glabrous or sparingly pubescent; petals white . . . . *L. nevadense*

— Ultimate segments of leaves 1–5 mm long, to 1 mm wide; leaves mostly with 5–8 opposite pairs of sessile or petiolulate lateral primary leaflets; root not as above; bractlets of the involucel pubescent; petals yellow, rarely white 14

14(13). Petals and anthers yellow; leaves often conspicuously ternate-pinnately compound, the lowest pair of primary leaflets nearly sessile or on petiolules to 5 cm long, some of these often arising directly from a dilated sheath with the petiole lacking or only to 2.5 cm long; plants common . . . . *L. foeniculaceum*

— Petals white; anthers purple or whitish; leaves pinnately or scarcely ternate-pinnately compound, the lowest pair of primary leaflets sessile or on petiolules to 1.5 cm long, these rarely arising directly from a dilated sheath, but rather from a petiole 1–4 (6) cm long; plants apparently rare, known only from western Millard County . . . . *L. ravenii*

15(10). Lowest pair of primary leaflets less than 1/3 as long as the leaf blade, sessile or on petiolules to 1.2 cm long; leaves strictly basal, the blades never arising directly from dilated sheaths; plants clothed at the base with old long-persisting leaf bases, of the southern 1/2 of the state 16

— Lowest pair of primary leaflets 1/3 to 3/4 as long as the leaf blade, sessile or on petiolules to 7.5 cm long; leaves basal and sometimes a few on the lower part of stems, the blades often arising directly from dilated sheaths; (plants not clothed at the base with old leaf bases and of the northern 1/2 of the state except sometimes in distribution of *L. grayi*) 18

16(15). Mature pedicels 1–10 mm long; fruit 4–9 mm long; leaves and peduncles scabrous, the blades 2–7 cm long; plants of the Great Basin and Washington County . . . . *L. scabrum*

— The longer mature pedicels 10–20 mm long; fruit (6) 8–20 mm long; leaves and peduncles glabrous or plants of the Colorado Basin 17

17(16). Leaf blades 3–7 cm long, the ultimate segments 2–4 mm long; fruit 8–10 mm long; rays 4–6, 1–3 cm long; plants densely scabrous, 10–15 cm tall, of western Colorado, to be expected in Utah in extreme eastern Grand and San Juan counties . . . . *L. eastwoodeae* (Coult. & Rose) Macbr.

— Leaf blades 7–24 cm long, the ultimate segments 1–15 mm long; fruit to 20 mm long; plants glabrous, glaucous, 8–40 cm tall, of the Colorado Basin and Washington County . . . . *L. parryi*

18(15). Bractlets of the involucel broadly elliptic to obovate, to 3 mm wide; pedicels 1–2 mm long; ultimate segments of leaves 2–13 mm long, 0.5–4 mm wide, dimorphic, plants of northwestern Box Elder County . . . . . . *L. cous*

— Bractlets of the involucel linear to subulate, not over 1 mm wide; pedicels 2–18 mm long; ultimate segments of leaves 1–7 mm long, 0.2–1.5 mm wide, not much if at all dimorphic 19

19(18). Petals white or cream; ultimate segments of leaves 0.5–1.5 mm wide; plants not aromatic; pedicels 3–16 mm long; leaves with 3–6 opposite pairs of lateral primary leaflets; rare glabrous forms . . . . *L. juniperinum*

— Petals yellow when fresh; ultimate segments of leaves 0.6–0.2 mm wide; plants strongly aromatic, glabrous; pedicels various; leaves various 20

20(19). Fruit 2–4 mm wide, the wings 0.4–0.6 mm wide; pedicels 2–5 mm long; rays very unequal; inflorescence open during flowering; leaves with 5–6 opposite pairs of lateral primary leaflets; plants not clothed at the base with old leaf bases, from a slender root, this often with 1 or more tuberlike segment . . . . *L. bicolor*

— Fruit 5–8 mm wide, the wings about 1.5–2 mm wide; pedicels 5–18 mm long; rays subequal; inflorescence congested at flowering time; leaves with about 7–10 opposite pairs of lateral primary leaflets; plants often clothed at the base with old long-persisting leaf bases, from a more or less woody branched caudex . . . . *L. grayi*

***Lomatium ambiguum* (Nutt.) Coult. & Rose** Wyeth Biscuitroot. [*Eulophus ambiguus* Nutt.]. Plants caulescent, 10–40 cm tall, glabrous without persisting leaf bases; root very slender, sometimes with 1 or more glabose or elongate tuberlike segments; leaves ternately or ternate-pinnately compound, petioles to 2 cm long or lacking and blades arising from a dilated sheath 1.5–4 cm long, blades 4–15 cm long, ovate in outline, lowest pair of primary leaflets mostly over 1/2 as long as the blade with petiolules 1–4 cm long, ultimate segments about 15–45, 0.3–9 cm long, 1–4 mm wide, often very unequal in the same leaf; peduncle 2.5–13 cm long; involucre lacking; rays 0.5–6.5 cm long, very unequal in the same umbel; involucel lacking; pedicels 2–12 mm long; petals and stamens yellow, fading in herbarium specimens; styles about 1 mm long; fruit 8–10 mm long, 2–3 mm wide, lateral wings about 0.5 mm wide, dorsal ribs filiform. Sagebrush and mountain brush communities at 1,525 to 1,980 m in Cache, Salt Lake, Utah, and Weber counties; Washington and adjacent British Columbia to Montana and south to Utah and Wyoming; 14 (0). The narrow fruits, unequal rays, and slender root with globose or elongate tuberlike segments are features also found in plants of *L. bicolor*, but the larger leaf segments are conspicuously different from the very narrow and shorter ones of plants of *L. bicolor*.

***Lomatium bicolor* (Wats.) Coult. & Rose** Wasatch Biscuitroot. [*Peucedanum bicolor* Wats.]. Plants 10–50 cm tall, acaulescent or caulescent, aromatic, glabrous, without persisting leaf bases or these few and weakly persisting; from a slender taproot, this often with one or more tuberlike segments; leaves ternate-pinnately decompound, petioles mostly lacking and the blades arising directly from a dilated sheath, blades 4–12 cm long, ovate in outline, finely and completely dissected, the lowest pair of primary leaflets mostly over 1/2 as long as the leaf blade, with petiolules 2.5–6 cm long, each with 5–6 opposite or offset pairs of secondary leaflets, ultimate segments mostly over 300, 1–4 (6) mm long, 0.2–0.6 mm wide; peduncle 10–28 cm long; rays 3–12 (20), 1–8 (11) cm long, very unequal in the same umbel; involucel lacking or of 1–8 linear separate bractlets; pedicels 2–5 mm long; petals and stamens yellow; styles about 1 mm long; fruit 8–11 mm long, 2–4 mm wide, congested; lateral wings 0.4–0.6 mm wide, dorsal ribs filiform. Sagebrush, mountain brush, aspen, and meadow communities at 1,525 to 2,438 m in Cache, Morgan, Rich, Salt Lake, and Weber counties; southeastern Idaho and northern Utah; 25 (0). This taxon has been included in *L. leptocarpum* (T. & G.) Coult. & Rose. Plants of the two taxa differ only in size of ultimate segments of leaves. Perhaps they are not distinct at the species level. *L. bicolor* has priority at the species level.

***Lomatium cous* (Wats.) Coult. & Rose** Cous Biscuitroot. [*Peucedanum cous* Wats.]. Plants 5–15 (25) cm tall, not or weakly aromatic, glabrous (ours), from a globose or fusiform tuberous root, this sometimes deep-seated and giving rise to a subterranean pseudoscape; leaves basal and sometimes 1–2 cauline on the lower 1/3 or rarely to midlength of the stem, 2–3 times pinnately or ternate-pinnately compound, blades 4–8 (11) cm long, mostly borne on dilated sheaths with the petioles obsolete or short or some leaves originating from the deep-seated tuber and then with etiolated, mostly subterranean petioles to 11 cm long, lowest pair of primary leaflets about 1/2 to over 3/4 as long as the leaf blade, sessile or with petiolules to 42 mm long, ultimate segments or lobes 2–13 mm long, 0.5–4 mm wide, as many as 200 or more, linear to elliptic; peduncles 1–7, 3–18 cm long; involucre lacking or of a solitary bract to 7 (10) mm long; rays 6–15, 0.4–5 cm long, strongly dimorphic in the same umbel; bractlets of the involucel about 6–10, 3–5 mm long, to 3 mm wide, broadly elliptic, ovate or obovate, greenish, sometimes with yellowish or scarious margins; pedicels 1–2 mm long; calyx teeth obsolete; petals and stamens yellow when fresh, fading to white in herbarium specimens; styles about 1.5 mm long; fruit 6–9 mm long, the lateral wings to about 1 mm wide, the dorsal ribs filiform or very obscurely winged. Sagebrush-grass communities at 2,440 to 2,560 m, in the Grouse Creek and Raft River Mountains, Box Elder County; Oregon to Montana, south to northwestern Utah and northeastern Nevada; 2 (ii).

Lomatium dissectum **(Nutt.) Mathias & Const.** Giant Lomatium. [*Leptotaenia dissecta* Nutt.]. Plants 30–130 cm tall, mostly short caulescent, puberulent or rarely glabrous, from a woody thickened taproot or caudex, without old leaf bases or these short-persistent and soon shredding; leaves pinnately or ternate-pinnately decompound, with 5–9 opposite or offset pairs of primary leaflets, or the upper cauline leaves much reduced, petioles 3–20 cm long, often lacking on cauline leaves and then the blades sessile on a dilated sheath, blades 10–30 cm long or smaller on cauline leaves, ovate in outline, the lowest pair of primary leaflets usually over 1/2 as long as the leaf blade, with petiolules 2.5–12 cm long, ultimate segments numerous, 1–12 mm long, 0.5–3 mm wide; peduncles 15–50 (90) cm long; involucre lacking or rarely of 1–3 rather quickly deciduous bracts; rays 9–27, 2–7 (12) cm long; bractlets of the involucel 3–6 mm long, or occasionally much longer and foliaceous; pedicels 3–10 (15) mm long; petals and stamens yellow, yellow-green, or purplish; styles about 1.5 mm long; fruit 9–15 (20) mm long, 6–10 mm wide, lateral wings about 1–2 mm wide, dorsal ribs filiform. Sagebrush, pinyon-juniper, oak-maple, aspen-fir, riparian, and rarely greasewood-desert shrub communities, from rock outcrops to deep loamy soil, at 1,280 to 2,650 (3,170) m in Beaver, Box Elder, Cache, Duchesne, Iron, Juab, Millard, Morgan, Rich, Salt Lake, Sanpete, Summit, Tooele, Uintah, Utah, Washington, and Weber counties; southern British Columbia and Alberta south to southern California, Arizona and Colorado; 91 (xiii). Utah materials are referable to **var. *eatonii* (Coult. & Rose) Cronq.** [*Leptotaenia eatonii* Coult. & Rose]. Sometimes the leaves are mistaken for those of *Ligusticum porteri*, but the mostly solitary umbel is strikingly different from the usually opposite or whorled lateral umbels in addition to the terminal one in the *Ligusticum*.

Lomatium foeniculaceum **(Nutt.) Coult. & Rose** Desert-parsley. [*Ferula foeniculacea* Nutt.]. Plants 5–25 (38) cm tall, acaulescent, densely pubescent throughout, from a more or less branching caudex and deep taproot, often clothed at the base with persisting leaf bases; leaves ternate-pinnately dissected, with 6–8 opposite pairs of lateral primary leaflets, petioles to 2.5 cm long or lacking and the blade arising from a dilated sheath, blades 2–13 cm long, completely and finely dissected, ovate in outline, the lowest pair of primary leaflets over 1/2 as long as the blade, sessile or with petiolules to 5 cm long, ultimate segments numerous, often more than 500, 1–3 (5) mm long, 0.5–1 (2.5) mm wide; peduncles 4–30 cm long; rays 5–20, 0.2–7 cm long; bractlets of the involucel 2–5 (6) mm long, separate or united at the very base, linear; pedicels 2–12 mm long; petals and anthers yellow (rarely white) when fresh and mostly remaining yellow for many years in herbarium specimens or occasionally turning purplish; styles about 1.5–2 mm long; fruit 5–10 mm long, 3–7 mm wide, lateral wings about 1–2 mm wide, dorsal ribs filiform. Sagebrush (mostly black sagebrush), pinyon-juniper, and mountain brush communities at 1,250 to 2,635 m in Beaver, Daggett, Box Elder, Emery, Juab, Kane, Millard, Sanpete, and Tooele counties; Manitoba to Missouri and Texas, west to southeastern Oregon and

California; 71 (xvi). Most Utah materials are referable to **var. *macdougalii* (Coult. & Rose) Cronq.** Some plants from western Utah with ciliolate petals are referable to var. *fimbriata* (Theobald) Boivin, but this feature seems variable in some populations.

***Lomatium grayi* (Coult. & Rose) Coult. & Rose** Milfoil Lomatium. [*L. millefolium* (Wats.) Macbr.]. Plants (8) 15–40 (80) cm tall, acaulescent or subcaulescent, strongly aromatic, glabrous, from a simple or branched caudex and thick taproot often clothed at the base with old, mostly shredded fibrous leaf bases; leaves ternate-pinnately dissected, with about 7–10 opposite pairs of lateral primary leaflets, petioles to 14 cm long or lacking and the blades arising from a dilated sheath 1–16 cm long, blades 7–16 (2) cm long, finely and completely dissected, ovate in outline, the lowest pair of primary leaflets from 1/2 to as long as the blade, with petiolules 1–7.5 cm long, ultimate segments several hundred or a thousand or more, extremely fine, 1–3 (6) mm long, 0.2–0.3 mm wide; peduncle 10–45 (70) cm tall; rays 10–26, 1.5–6 (8) cm long; bractlets of the involuces 3–5 mm long, linear, separate or united at the base; pedicels 5–13 (18) mm long; petals and stamens yellow when fresh, soon fading whitish when dried; styles 1.5–2.5 mm long; fruit 6–12 mm long, 5–8 mm wide, lateral wings about 2 mm wide, dorsal ribs filiform. With 2 intergrading but more or less geographically distinct varieties.

1. Fruit 6–9 (10) mm long, the lateral wings to about 1.5 mm wide; leaves rather openly dissected, with a few hundred ultimate segments; plants usually with greater buildup of old leaf bases that persist a little longer before shredding than in the following variety, averaging smaller, 8–20 (35) cm tall, of the western tier of counties from Box Elder County south to Beaver County .... *L. grayi* var. *depauperatum*

— Fruit 8–12 mm long, the lateral wings to about 2 mm wide; leaves with congested and numerous ultimate segments, these several hundred or a thousand or more; plants usually with less buildup of old persistent leaf bases, these usually shredding within a year, averaging larger, 15–40(80) cm tall, of more easterly distribution and only in the eastern 1/4 of the western tier of counties where more or less transitional with the preceding variety .... *L. grayii* var. *grayi*

Var. *depauperatum* (Jones) Mathias [*Cogswellia millefolia* var. *depauperata* Jones]. Desert shrub, pinyon-juniper, and mountain brush communities at 1,525 to 2,835 m in Beaver, Box Elder, Juab, Millard, and Tooele counties; western Utah and adjacent Nevada; 58 (xiii).

Var. *grayi* Sagebrush, pinyon-juniper, mountainbrush, ponderosa pine, and Douglas-fir communities at 1,340 to 2,745 m in Box Elder, Cache, Daggett, Davis, Duchesne, Grand, Juab, Morgan, Rich, Salt Lake, San Juan, Sanpete, Summit, Tooele, Uintah, Utah, and Weber counties; Washington to northeastern Nevada and east to Idaho and southwestern Colorado; 121 (xxiii)

***Lomatium junceum* Barneby & N. Holmgren** Rush-lomatium. Plants (6) 10–37 cm tall, acaulescent, glabrous, from a simple to much branched woody caudex, clothed at the base with old petioles, some of which often persist for a few years before shredding; leaves rushlike, trifid or pinnatifid or rarely reduced to a petiole and a linear bladeless rachis, with 1–7 linear segments, petioles 3–15 mm long with a short sheath at the base, blades 3–17 cm long, the segments 1–18 cm long, about 1–2 mm wide, terete and similar to the rachis and petioles in diameter; peduncles 5–25 cm long; rays of umbels 6–13, 1.5–3 cm long; bractlets of the involucel 1.5–3 mm long, separate or united at the base, linear; pedicels 4–11 mm long; calyx teeth to about 1 mm long, acutish, somewhat persistent; petals and stamens bright yellow or cream, quickly fading to white when frozen or dried; styles about 2–3 mm long; fruit 8–12 mm long, 5–7 mm wide, lateral wings 1–2 mm wide, dorsal ribs filiform. Desert shrub, sagebrush, pinyon-juniper, ponderosa pine, and Douglas-fir communities at 1,615 to 2,485 m in Emery, Garfield, Sevier, and Wayne counties; endemic; 21 (iii).

***Lomatium juniperinum* (Jones) Coult. & Rose** Juniper Lomatium. [*Peucedanum juniperinum* Jones]. Plants 8–32 cm tall, acaulescent or with 1–3 leaves on the lower part of the stems, more or less hirtellous, occasionally glabrate and rarely glabrous, often with a short pseudoscape, from a taproot with simple or sparingly branched crown, not clothed at the base with old leaf bases or these weakly persisting; leaves ternate-pinnately dissected, with (3)4–6 opposite or offset pairs of lateral primary leaflets, petioles to 8 cm long or lacking and the blades arising directly from dilated sheaths 1–4 cm long, blades 2.5–8 (11) cm long, ovate in outline, the lowest pair of lateral primary leaflets 1/3 to about as long as the leaf blade, with petiolules to 3 cm long, the ultimate segments about 50–400, 1–7 mm long, 0.7–1.5 mm wide; peduncles 6–29 cm long; rays of the umbel 3–12, 1–8 cm long; bractlets of the involucel about 1–5, 1–4.5 mm long, linear, separate or united at the base; pedicels 3–16 mm long; petals white, cream, or yellow; anthers white, ochroleucus, purple, or yellow; styles about 1–2 mm long; fruit 5–8 (11) mm long, 3–6 mm wide, glabrous, or scabrous to sparsely hirtellous especially when young; lateral wings 0.5–1.5 mm wide, the dorsal ribs filiform. Sagebrush, pinyon-juniper, forb-grass, aspen, Douglas-fir, and alpine (Mt. Nebo) communities at 1,830 to 3,230 m in Carbon, Daggett, Duchesne, Grand, Juab, Sanpete, Summit, Uintah, Utah, and Wasatch counties; southwestern Wyoming and adjacent Idaho to Utah and extreme northwestern Colorado; 50 (xviii). Quite variable as to color of petals and anthers. Plants with yellow petals and anthers are known only from the west and north side of the Uinta Mountains and West Tavaputs Plateau. Those with white petals and white to purplish anthers are found in the Wasatch Mountains, south slope of the Uinta Mountains, Tavaputs Plateau, and to the north end of the Wasatch Plateau. Plants are quite pubescent except a few specimens from the Wasatch Mountains and Wasatch Plateau. The plants are sometimes confused with those of *L. nevadense*. The following key and discussion should help separate the two taxa.

1. Leaves ternate-pinnately compound, the lowest pair of primary leaflets on petiolules mostly 1–3 cm long; plants of northern Sanpete County and northward and eastward .... *L. juniperinum*

— Leaves pinnately compound, the lowest pair of primary leaflets sessile or on petiolules mostly less than 1 cm long; plants of Millard County and southward and westward .... *L. nevadense*

In Utah the difference is more obvious because most of the Utah plants of *L. nevadense* have: usually densely hirtellous or puberulent ovaries and young fruits, with the pubescence often remaining in some of the mature fruits; ultimate segments of leaves about 20–100, dimorphic, with the larger ones 7–27 mm long, and slender roots with fusiform tuberous enlargements. Plants of *L. juniperinum* have: glabrous or scabrous ovaries and young fruits, with the scabrousity lacking or scattered in mature fruits; ultimate segments of leaves 50–400, 1–7 mm long, and the root does not have tuberous enlargements. Sometimes the plants are also confused with those of *Cymopterus lemmonii*. (q.v.)

Lomatium latilobum **(Rydb.) Mathias** Canyonlands Lomatium. [*Cynomarathrum latilobum* Rydb.]. Plants (6) 10–30 cm tall, acaulescent, glabrous, from a branched woody caudex, clothed at the base with old persistent leaf bases; leaves pinnate with 3–4 (5) pairs of lateral leaflets; petioles 2–16 cm long; blades 1–10 cm long, oblong in outline, leaflets 1–4 cm long, 2–12 mm wide, sessile, entire or a few bifid or trifid; peduncles 4–27 cm long; rays of the umbel 4–13, 0.5–2 cm long; bractlets of the involucel 2–15 mm long, 0.5–2 mm wide, linear or elliptic, separate; pedicels 1–4 mm long; calyx teeth 1–1.5 mm long, acute; petals yellow when fresh, drying white; styles 2–3 mm long; fruit 8–12 mm long, 3–7 mm wide, the lateral wings about 1 mm wide, the dorsal ribs filiform. Pinyon-juniper communities, and in hanging gardens, sandstone ledges, and sandy soil, at ca 1,525 m, in southern Grand and adjacent San Juan counties, also Mesa County, Colorado; 17 (i).

Lomatium macrocarpum **(H. & A.) Coult. & Rose** Big-seed Lomatium. [*Ferula macrocarpa* H. & A.]. Plants 12–30 cm tall, acaulescent or subcaulescent with leaves mostly on the lower 1/4 of the stem, more or less tomentose-villous or glabrate, from a thickened taproot with a simple or sparingly branched crown with few or no persisting leaf bases; leaves pinnately or ternate-pinnately dissected, with about 4 opposite pairs of lateral primary leaflets, petioles often long tapering into a dilated sheath, the petiole and sheath about 3–6 cm long, blades 3–6 cm long, ovate in outline, the lowest pair of primary leaflets 1/2 to 3/4 as long as the leaf blade, sessile or with petiolules to 1 cm long, ultimate segments about 30–300 or more, 1.5–6 mm long, 0.5–2 mm wide, elliptic or linear; peduncles 8–26 cm long; rays of the umbel 6–18, 1–4 (6.5) cm long; bractlets of the involucel about

10, 2–10 mm long, separate or united at the base, pubescent; pedicels 2–5 mm long; calyx teeth to about 0.5 mm long; petals white or purplish in age; anthers white; styles about 2–3 mm long; fruit 9–12 (15) mm long, 4–5 mm wide, glabrous, the lateral wings 1–1.5 mm wide, the dorsal ribs filiform. Desert shrub, sagebrush, and pinyon-juniper communities at 1,480 to 2,550 m in Daggett, Juab, Millard, Sanpete, Tooele, and Uintah counties; southern British Columbia to California and east to Manitoba and Colorado; 29 (xi).

***Lomatium minimum* (Mathias) Mathias** Least Lomatium. [*Cogswellia minima* Mathias]. Plants 2–12 (17) cm tall, acaulescent, glabrous or scabrous, from a branched caudex, the caudex branches clothed with persisting leaf bases; leaves once-pinnatifid or rarely trifid, with (3) 5–9 (13) segments, petioles to 2 cm long, blades 1–2.5 cm long, the segments 2–15 (20) mm long, 0.5–2 mm wide; peduncles to 10 (16) cm long; rays of the umbel 3–6, 0.3–2.3 (3.2) cm long; bractlets of the involucel 2–4 mm long, linear-subulate, separate; pedicels 1–3 mm long; calyx teeth to 0.6 mm long, acute, greenish or purplish in age with scarious margins; petals and stamens yellow, drying to cream; styles about 1.5–2 mm long; fruit 4–7 mm long, 3–4 mm wide, lateral wings 0.5–1 mm wide, dorsal ribs mostly filiform. Forb-grass, ponderosa pine, and bristlecone pine communities, often on exposed ridges and raw escarpments, often on limestone at 2,165 to 3,170 m in Garfield, Iron, and Kane counties; endemic; 20 (0). Appearing much like a diminutive form of *L. nuttallii* var. *alpinum*.

***Lomatium nevadense* (Wats.) Coult. & Rose** Nevada Lomatium. [*Peucedanum nevadense* Wats.]. Plants 10–36 cm tall, acaulescent or with 1 or 2 leaves on the lower part of stems, more or less pubescent throughout, from a slender root frequently with a fusiform tuberous segment, with or without persisting leaf-bases; leaves 2–3 times pinnately compound, with about 4 opposite pairs of lateral primary leaflets, petioles to 7.5 cm long or often lacking and the blade sessile on a dilated sheath, blades 2.5–9 cm long, ovate in outline; the lowest pair of primary leaflets about 1/2 to nearly as long as the blade, sessile or on petiolules to 5 mm long, the ultimate segments about 20–80, 1–27 mm long, 0.5–3 mm wide; peduncles 7–33 cm long; rays of the umbel 7–12, sometimes with as few as 3 of them fertile, 1.5–4 cm long; bractlets of the involucel 2–3 mm long, lanceolate, linear-elliptic, or narrowly obovate; pedicels 4–11 mm long; petals and stamens white; styles about 1–1.5 mm long; fruit 5–10 mm long, 3–7 mm wide, densely puberulent or rarely glabrous when young to glabrate; lateral wings 0.8–2 mm wide, dorsal ribs filiform. Desert shrub, sagebrush, pinyon-juniper, mountain brush, and ponderosa pine communities at 1,524 to 2,285 m in Beaver, Garfield, Iron, Kane, Millard, and Washington counties; Oregon to California east to Colorado and Arizona; 44 (viii). Our materials are perhaps referable to var. *parishii* (Coult. & Rose) Jepson [*Peucedanum parishii* Coult. & Rose]. This variety has been keyed as having glabrous fruits, and the Utah materials with pubescent fruits have been referred to as var. *nevadense*. However, the Utah plants have dimorphic ultimate leaf segments 1–27 mm long. This is a feature of var. *parishii*. The ultimate leaf segments of var. *nevadense* are only 2–3 mm long. A specimen from Navajo Mountain, San Juan County (Albee 4463 UT), has uniformly small leaf segments and glabrous fruits.

***Lomatium nudicaule* (Pursh) Coult. & Rose** Naked-stem Lomatium. [*Smyrnium nudicaule* Pursh]. Plants 20–45 cm tall, acaulescent, glabrous, from a taproot, without persistent leaf bases or these few and weakly persisting; leaves ternate or biternate; with 3–11 distinct leaflets, petioles to 6 cm long, or obsolete and the blades arising from a dilated sheath, blades 4–10 cm long, ovate in outline, leaflets 2–5 cm long mostly 1–5.5 cm wide, ovate or orbicular to reniform, coarsely toothed toward the apex; peduncles 15–27 cm tall, sometimes swollen at the apex; rays of the umbel 7–27, 8–10 cm long; involucel lacking; pedicels 3–10 mm long; petals yellow; styles about 1–2 mm long; fruit 8–12 mm long, 2–5 mm wide, the lateral wings about 0.5 mm wide, dorsal ribs filiform. Sagebrush, pinyon-juniper, and mountain brush communities at 1,585 to 2,530 m in Box Elder, Juab, and Tooele counties; southern British Columbia to central California and east to southwestern Alberta and Utah; 6 (iii).

***Lomatium nuttallii* (Gray) Macbr.** Stinking Lomatium. Plants 15–50 cm tall, acaulescent, glabrous, strongly aromatic, from a branched caudex, the caudex clothed with persistent leaf bases; leaves pinnatifid to bipinnate or ternate-pinnately compound, petioles gradually expanded into a dilated sheath, with the sheath 2–21 cm long, blades 2–15 cm long, usually oblong in outline, ultimate leaflets or segments about 7–30, 0.3–6.5 cm long, 0.5–2 (4) mm wide; peduncles 12–47 cm long; rays of the umbel (3) 5–12, 1–5 cm long; bractlets of the involucel 3–10 mm long; pedicels 2–10 mm long; calyx teeth about 0.5 mm long, rather scarious; petals and stamens yellow, soon turning pale to white in herbarium specimens; styles about 2–3 mm long; fruit 5–15 mm long, 3–5 mm wide, lateral wings about 0.5–1 mm wide, the dorsal ribs filiform or somewhat prominent with rudimentary wings. There are two geographically separated varieties that are distinct morphologically, but some of the smaller specimens of var. *nuttallii* are much like those of var. *alpinum*. They are separated as follows:

1. Fruit 5–8 mm long, the lateral wings ca 0.5 mm wide; pedicels 4–10 mm long; umbels with only 3–6 rays; leaves once pinnatifid with sessile segments or some of the lower pairs of segments bipinnatifid; plants of Washington and western Millard counties .... *L. nuttallii* var. *alpinum*

— Fruit 10–15 mm long, the lateral wings about 1 mm wide; pedicels 2–6 mm long; umbels with up to 12 rays; leaves pinnatifid to ternate-pinnately compound, with the lowest pair of primary leaflets on petiolules (1) 2.5–9 cm long; plants of Sevier and eastern Millard counties and northward . *L. nuttallii* var. *nuttallii*

Var. *alpinum* (Wats.) Mathias Pinyon-juniper and mountain brush communities at 2,225 to 2,440 m in Millard and Washington counties; western Nevada and southwestern Utah; 4 (0).

Var. *nuttallii* [*Peuceda-num graveolens* Wats.]. Sagebrush, bullgrass, mountain brush, Douglas-fir, limber pine, and spruce-fir communities, often in rocky places, mostly on limestone and other basic substrates, sometimes in raw snowflush areas, at 1,980 to 3,200 m in Cache, Davis, Duchesne, Millard, Rich, Salt Lake, Sanpete, Sevier, Summit, Tooele, Utah, Wasatch, and Weber counties; western Nevada, and western Wyoming; 85 (xviii).

***Lomatium parryi* (Wats.) Macbr.** Parry Lomatium. [*Peucedanum parryi* Wats.; *Cogswellia cottami* Jones]. Plants 8–40 cm tall, acaulescent, glabrous, from a branched caudex, clothed at the base with persisting leaf bases; leaves bipinnatifid or partly tripinnatifid, with mostly 7–9 opposite pairs of primary leaflets or the upper leaflets simple, petioles 3–16 cm long, terete, often persisting for a few years without shredding, blades 7–24 cm long, lowest pair of lateral primary leaflets 1/10–1/4 as long as the leaf blade, sessile or with petiolules to 1.2 cm long, the ultimate segments mostly 50–150, 1–15 mm long, 1–2 mm wide, acute; peduncles 5–32 cm long; rays of the umbel 8–13, 1–5 cm long; bractlets of the involucels 3–10 mm long, entire, tridentate or rarely pinnatifid, spreading to reflexed in age; pedicels 1–2 cm long; petals yellow, turning white in herbarium specimens; styles about 2–4 mm long; fruit 6–20 mm long, 5–10 mm wide, the lateral wings 1–3 mm wide, the dorsal ribs filiform. Desert shrub, blackbrush, pinyon-juniper, and mountain brush communities at 975 to 2,320 m in Emery, Garfield, Grand, Iron, Kane, San Juan, and Washington counties; Utah to eastern California; 65 (v).

***Lomatium ravenii* Mathias & Const.** Raven Lomatium. Plants 4–23 cm tall, acaulescent, densely hirtellous throughout, from a taproot, with a simple or branched crown, usually clothed at the base by shredded leaf bases; leaves ternate-bipinnate or 2–3 times pinnately dissected, with 5–7 (8) opposite pairs of primary leaflets, petioles to 6 cm long or lacking and blades arising from dilated sheaths to 2 cm long, blades 1.5–8 cm long, finely and completely dissected, the lowest pair of primary leaflets usually over 1/2 as long as the leaf blade, sessile or with petiolules to 1.5 cm long, the ultimate segments about 300–600 or more, 1–5 mm long, 0.5–1 mm wide; peduncles 2.5–21 cm long; rays of the umbel nearly obsolete or to 3.7 cm long; bractlets of the involucel 1–3 mm long, linear, pubescent; pedicels 1–8 mm long; petals white; anthers purple; styles about 1–2 mm long; fruit 6–10 mm long, 3–6 mm wide, pubescent, the lateral ribs with wings 0.5–1 mm long, dorsal ribs filiform. Pinyon-juniper-mahogany communities, at ca 2,380 m in western Millard County; Great Basin from southeastern Oregon and southwestern Idaho to northern California, central Nevada and western Utah; 1 (i). Except for the white petals, purple anthers and sometimes slightly less pubescent foliage, plants of this taxon could pass for plants of *L. foeniculaceum*. Fruiting specimens may be difficult to distinguish.

Lomatium scabrum **(Coult. & Rose) Mathias** Rough Lomatium; Cliff Lomatium. [*Cynomarathrum scabrum* Coult. & Rose]. Plants 6–25 (34) cm tall, acaulescent, mostly scabrous, from a branched caudex, clothed at the base by persistent leaf bases; leaves bipinnately to tripinnately dissected, with (5) 7–11 opposite pairs of lateral primary leaflets, petioles 1–7 (10) cm long, blades (1.5) 2–11 cm long, lowest pair of primary leaflets less than 1/3 as long as the leaf blade and seldom over 1/4 as long, sessile or nearly so, the ultimate segments about 50–400 or more, 1–4 mm long, 0.4–2 mm wide; peduncles 5–25 (32) cm long; rays of the umbel 4–11, 0.5–2 (3) cm long; bractlets of the involucel 1–4 mm long, linear; pedicels 1–5 (10) mm long; petals and stamens mostly yellow or occasionally white when fresh, fading white in herbarium specimens; styles about 2–3 mm long; fruit 4–7 mm long, 3–4 mm wide, the lateral wings to 1 mm wide, the dorsal ribs filiform or sometimes with a rudimentary wing at the base. There are 2 intergrading varieties as follows:

1. Leaves mostly bipinnately dissected, with about 50–110(140) ultimate segments; fruit 4–8 mm long; plants mostly found above 1,615 m *L. scabrum* var. *scabrum*

— Leaves tripinnately dissected, with about 150–400 or more ultimate segments; fruit 6–9 mm long; plants mostly found below 1,615 m . . . . *L. scabrum* var. *tripinnatum*

Var. *scabrum* Desert shrub, pinyon-juniper, mountain brush, and white fir communities, mostly on limestone and dolomite outcrops at 1,615 to 2,684 m in Beaver, Iron, Juab, and Millard counties and adjacent Nevada; 55 (xii). Some specimens, especially from Iron County, are wholly transitional to the following variety.

Var. *tripinnatum* Goodrich, var. nov. Similis *Lomatio scabro* var. *scabro* sed foliis tripinnatifidis et segmentis ultimo plus numerosis differt. HOLOTYPE: Utah. Washington Co., T41S, R16W, Sec 10, SE1/4, 14.2 km 340 degrees NW of St. George, Lava Ridge-Snow Canyon, 1,280 m elev., *Mahonia-Fraxinus-Coleogyne-Arctostaphylos* comm., on sandstone, 8 May 1984, S. Goodrich 20282 (BRY); isotypes ARIZ, RM, CAS, UC, POM, NY, UT, UTC, MO, US, WS. Additional specimens: Washington Co., T41S, R17 W, Sec 8, NE1/4, 22.5 km 309 degrees NW of St. George, 8 May 1984, S. Goodrich 20268 (ARIZ, BRY, CAS, MO, NY, POM, RM, UC, US, WS). Blackbrush and pinyon-juniper communities, often on sandstone or in sandy places at 792 to 1,475 (2,170) m, in Washington County; and adjacent Arizona; 29 (ii).

Lomatium triternatum **(Pursh) Coult. & Rose** Ternate Lomatium. [*Seseli triternatum* Pursh]. Plants 20–70 cm tall, acaulescent or subcaulescent, mostly hirtellous throughout except on the fruit, from a taproot with simple or sparingly branched crown, not clothed at the base with persistent leaf bases or only weakly so; leaves ternate-pinnately compound with (3) 9–21 leaflets or segments, petioles up to 23 cm long including the dilated sheathing base, or reduced to the sheath; blades 4–20 cm long, ovate in outline, the lowest primary leaflets often over 1/2 as long as the leaf blade, ultimate leaflets or segments 1–13 cm long, 1–15 mm wide; peduncles 15–55 cm long; rays of the umbel 4–20, 2–10 cm long; bractlets of the involucel about 6–10, 1–10 mm long, about 0.1–0.5 mm wide; pedicels 2–7 mm long; petals and stamens bright yellow when fresh but fading to white in herbarium specimens; styles about 1–1.5 mm long; fruit 8–15 mm long, 4–11 mm wide, the lateral wings 1–2.5 (4) mm long, the dorsal ribs filiform. There are 2 subspecies. In Utah they can be separated as follows:

1. Ultimate leaflets or segments linear, over 10 times as long as wide, to 13 cm long, 1–6 (10) mm wide; fruit broadly elliptic, the mature wings as broad or nearly as broad as the body . . . . *L. triternatum* ssp. *platycarpum*

— Ultimate leaflets elliptic, 3–9 times as long as wide, 2–6 cm long, (3) 6–15 mm wide; fruit rather narrowly elliptic to nearly linear, the mature wings seldon more than half as wide as the body. . . . . . L. *triternatum* ssp. *triternatum*

Ssp. *platycarpum* (Torr.) Cronq. [*L. simplex* (Nutt.) Macbr.]. Sagebrush-grass, pinyon-juniper, mountain brush, ponderosa pine, lodgepole pine, and dry meadow communities at 1,310 to 2,895 m in Box Elder, Cache, Daggett, Duchesne, Morgan, Rich, San Juan, Summit, Uintah, Utah, Wasatch, and Weber counties; southern British Columbia and Montana to Idaho and Colorado; 116 (viii).

Ssp. *triternatum* Mountain brush and aspen communities, sometimes on heavy clay soils with *Wyethia* at 1,580 to 2,590 m in Weber and Summit counties; southern Alberta and British Columbia to Utah; 8 (0). Utah specimens are referable to **var.** *anomalus* (Jones) Cronq. [*L. anomalum* Jones].

Musineon Raf.

Perennial plants with leaves mostly at or near the base, from a thickened taproot with a simple or branched crown or caudex; leaves 1 or more times pinnately or ternate-pinnately compound; umbel compound; involucre usually lacking; involucel of several separate or basally united bractlets; calyx teeth well developed, ovate; petals and stamens white or yellow; stylopodium lacking; carpophore entire to deeply cleft; fruit ovoid to linear oblong, somewhat laterally compressed, evidently ribbed.

Musineon lineare **(Rydb.) Mathias** Rydberg Musineon. [*Daucophyllum lineare* Rydb. *Aletes tenuifolia* Coult. & Rose]. Plants 5.5–25 cm tall, caulescent or subcaulescent, glabrous, from a mostly branched caudex, more or less clothed at the base with long-persisting leaf bases; leaves mostly on the lower 1/3 of the plants, ternate or more often pinnate, with 2–4 opposite pairs of lateral leaflets, petioles 0.5–6 (14) cm long, blades 1–5.3 cm long; leaflets, sessile, entire or bifid, trifid or rarely pinnatifid, ultimate leaflets or lobes 3–20 mm long; peduncles 5–22 cm long, very slender; umbel solitary; rays about 5–10, 1–5 mm long; involucels of about 3 linear or narrowly elliptic bractlets 4–10 mm long; pedicels about 1 mm long; calyx teeth about 0.5 mm long, greenish or purplish with scarious margins; petals and stamens white; styles about 1 mm long; fruit 2–4 mm long, minutely scabrous, the ribs evident but not winged. Limestone cliffs in the Bear River Range, Cache County; endemic; 4 (0).

Oreoxis Raf.

Caespitose, acaulescent herbs from branched woody caudices, these usually clothed with long-persisting leaf bases; leaves pinnate or bipinnate; umbels compound; involucre mostly lacking; bractlets of the involucel more or less united at the base, usually exceeding the flowers; calyx teeth conspicuous; petals and stamens yellow at least when fresh; stylopodium lacking; carpophore lacking; fruit oblong to ovoid-oblong, slightly compressed laterally, the ribs corky-winged. Plants of the genus could reasonably be included in *Cymopterus*, and with the recent discovery of the low elevation *O. trotteri* such inclusion will probably be necessary.

1. Bractlets obovate, toothed at the apex, usually purplish, plants of the La Sal Mountains . . . . *O. bakeri*

— Bractlets linear or narrowly elliptic, entire, acute to acuminate; plants more widely distributed 2

2(1). Plants pulvinate caespitose, forming clumps to 30 cm wide, from low elevations in Grand County; caudex clothed with a thatch of terete leaf bases; ultimate segments elliptic to cuneate-ovate . . . . *O. trotteri*

— Plants caespitose but hardly pulvinate, from high elevations, widespread; caudex clothed with short, more or less flattened leaf bases; ultimate segments of leaves linear to linear-elliptic . . . . *O. alpina*

Oreoxis alpina **(Gray) Coult. & Rose** Alpine Oreoxis [*Cymopterus alpinus* Gray]. Plants 2.5–11.5 cm tall, scabrous-hirtellous throughout, from a branched caudex, the caudex clothed with persisting leaf bases; leaves all basal, mostly bipinnate, with ca 4 opposite pairs of sessile or nearly sessile lateral primary leaflets, the upper pairs and those of smaller leaves sometimes once pinnate and then trifid to pinnatifid, petioles 0.5–2.5 cm long, blades 1–3.5 cm long oblong in outline, lowest pair of primary leaflets 4–14 mm long, the ultimate segments about 1–6 mm long, 0.4–1.5 mm wide, linear to narrowly elliptic; peduncles 2–10.5 cm long; umbel solitary; involucre lacking; rays 4–7, 1–6 mm long; involucels of 5–9 bractlets 1–4 mm long, united at the base; pedicels obsolete or to about 0.3 mm long; calyx teeth 0.6–1 mm long, green; petals and stamens yellow when fresh, fading to white or cream or purple tinged within a few years in herbarium specimens; styles 1.7–2 (3) mm long; fruit 4–5 mm long, the ribs with low corky wings to about 0.7 mm wide. Forb-grass, limber pine, spruce, and alpine communities, and raw escarpments and barren ridges at 2,440 to 3,475 m in Duchesne, Garfield, Grand, San Juan, Sanpete, Summit, and Wayne counties; Wyoming to New Mexico and Arizona; 27 (vi).

***Oreoxis bakeri* Coult. & Rose** Plants 1–12 cm tall, slightly puberulent at base of umbels and rays; leaves basal, bipinnate for the most part or pinnate with pinnatifid or trifid leaflets, with 3–4 opposite pairs of lateral primary leaflets, the petioles 0.8–2.5 cm long; blades 0.8–5 cm long, lowest pair of primary leaflets to about 1 cm long, sessile or nearly so, the ultimate segments to 7 mm long, to 1 mm wide; peduncles 1–11 cm long; umbels solitary, involucre lacking; rays 3–8, 3–5 mm long; bractlets of the involucel united at base, 3–5 mm long, nearly linear-elliptic to obovate, usually 3–toothed at the apex; petals and stamens yellow at least when fresh; styles to about 1 mm long; fruit 2–4 mm long, the ribs with low corky wings to 0.75 mm wide. Alpine forb-grass communities, at ca 3,660 m, La Sal Mountains, in Grand and San Juan counties; Colorado, Utah, and New Mexico; 4 (0).

***Oreoxis trotteri* Welsh & Goodrich** Plants pulvinate-caespitose, forming clumps to 30 cm wide, 4–8 cm tall, scabrous and more or less glandular, from a branching caudex, this clothed with a thatch of persistent, terete leaf bases and peduncles; leaves all basal, bipinnate, with ca 4 opposite pairs of sessile, lateral, primary leaflets, the upper pairs and those of the smaller leaves sometimes once-pinnate and then trifid or pinnatifid; petioles 1–3.5 cm long; blades 1.5–2.3 cm long, oblong in outline, the lowest pair of primary leaflets 3.5–5 mm long, the ultimate segments 1–3.5 mm long, 1–3 mm wide, elliptic to cuneate-ovate; peduncles 4–7.5 cm long; umbel solitary; involucre lacking; rays 5–7, 3–5 mm long; involucels of 4–7 linear-subulate bractlets 2–3.5 mm long, distinct or essentially so; pedicels obsolete or to ca 1 mm long; calyx teeth ca 1 mm long, green or purplish; petals and stamens yellow; styles 1–1.2 mm long; fruit 2.8–4.8 (5) mm long, the ribs with low, corky wings to 0.7 mm wide. Mixed juniper and warm desert shrub community at ca 1,464 m in Grand County; endemic; 2 (0).

Orogenia Wats.

Perennial acaulescent glabrous low herbs from a fusiform or globose root; leaves ternate or biternate with linear entire leaflets; umbel compound; involucre lacking or of a few linear minute scarious bractlets; calyx teeth obsolete; petals and stamens white or purplish; stylopodium lacking; carpophore lacking; fruit oblong to oval, nearly round in cross section, the dorsal ribs evident or obsolete, the lateral ones corky-winged but inflexed into the commissure, a corky riblike projection also running the length of the commissural faces of each mericarp.

***Orogenia linearifolia* Wats.** Indian Potato. Plants 5–10 (13) cm tall, glabrous, not aromatic, from a globose or fusiform root, with a fragile etiolated subterranean pseudoscapelike stem easily detached from the tuberous root; leaves borne at ground level or a few arising from the tuberous root with etiolated petioles, ternate or biternate, blades 3–8 (12.5) cm long, the 3–9 leaflets 1.5–5 (11.5) cm long, 1–11 mm wide, linear, entire, the lowest pair of petiolules to 2 cm long; peduncles 3–8 cm long, usually a little longer than the subterranean stem; involucre lacking; rays 3–12, but rarely more than 5 of them fertile, 0.3–3 cm long; involucel proper apparently lacking, but some of the pedicels usually bearing a linear bractlet to 4 mm long; pedicels nearly obsolete or to 2 mm long; petals white; filaments white, anthers pale or dark purple; styles about 1 mm long; fruit about 4–6 mm long; dorsal ribs filiform. Sagebrush-grass, oak, maple, aspen, ponderosa pine, white fir, and rarely desert shrub communities, mostly flowering at the edge of melting snow at 1,370 to 2,805 m in Beaver, Box Elder, Juab, Millard, Morgan, Salt Lake, San Juan, Sanpete, Sevier, Summit, Tooele, Uintah, Utah, Wasatch, Washington, and Weber counties; Washington to Montana, south to Utah and Colorado; 50 (vii).

Osmorhiza Raf.

Perennial caulescent usually pubescent herbs from taproots with simple or branched crowns; leaves ternately or pinnately 1–3 times compound with well-marked leaflets; umbels compound; involucre lacking or of 1 or a few narrow foliaceous bracts; involucel lacking or of several foliaceous reflexed bractlets; calyx teeth obsolete; petals and stamens white, greenish white, yellow, pink, or purple; stylopodium, conic to depressed; carpophore bifid less than 1/2 its length; fruit linear or clavate, somewhat compressed laterally, bristly hispid to glabrous, the ribs narrow.

1. Ovaries and fruit glabrous, generally obtuse at both ends; petals and stamens yellow or greenish yellow; leaves (1)2 times pinnately or ternate-pinnately compound; plants strongly aromatic, usually with more than 2 stems . . . . *O. occidentalis*
— Ovaries and fruit bristly hispid, with long, pointed bristly hispid tails; petals white or greenish white; leaves biternate; plants not strongly aromatic, often with solitary stems . . 2
2(1). Mature fruit including tails mostly 16–25 mm long, the apex concavely pointed into a 1–2 mm long beak; the most divergent rays spreading 30 degrees to 65 degrees from the peduncle; fruiting pedicels mostly ascending-spreading; plants most common below 2,470 m elev . . . . *O. chilensis*
— Mature fruit including tails mostly 13–18 mm long, the apex convex and obtuse; the most divergent rays spreading 40 degrees to 90 degrees from the peduncle; fruiting pedicels horizontally spreading to ascending; plants common above as well as below 2,470 m . . . . *O. depauperata*

***Osmorhiza chilensis* H. & A.** [*O. nuda* Torr.]. Stems often solitary, 18–75 cm tall, from a taproot, without long-persisting leaf bases; herbage not strongly aromatic; leaves basal and 2–3 cauline, biternate, usually with 9 distinct leaflets, petioles about 3–16 cm long, or cauline leaves sessile, blades 5–15 cm long, lateral primary leaflets about as long as the central one, with petiolules (1) 2–5.5 cm long, blades of leaflets 1–4 (5.5) cm long, elliptic to ovate, lobed to cleft, and toothed, ciliate and often pubescent on nerves below and sometimes scattered pubescent between the nerves; peduncles 5–34 cm long; umbels 1–5; involucre lacking; rays 3–7, 2.5–9 (13) cm long, ascending or spreading-ascending, glabrous to hirtellous; involucels lacking; pedicels 5–22 (30) mm long, ascending; petals and stamens greenish white; styles less than 0.5 mm long; fruit, including the tails, 16–25 mm long, linear-clavate, bristly-hispid, the beak concavely pointed, 1–2 mm long, the concave beak usually evident in young fruits. Oak, maple, aspen, Douglas-fir, white fir, narrowleaf cottonwood, and riparian communities at 1,520 to 2,470 (2,680) m in Box Elder, Cache, Daggett, Davis, Duchesne, Juab, Millard, Salt Lake, Sanpete, Tooele, Uintah, Utah, Wasatch, Washington, and Weber counties; Alaska to California, east to Alberta and Arizona, also Great Lakes region and in Argentina and Chile; 54 (viii). See *O. depauperata*.

***Osmorhiza depauperata* Phil.** Blunt-fruit Sweet-cicely. [*O. obtusa* (Coult. & Rose) Fern.]. Stems mostly solitary, 14–63 (77) cm tall, often with a slight ring of hairs at the nodes, from a taproot, without persisting leaf bases; herbage not strongly aromatic; leaves basal and 1–3 cauline, biternate, usually with 9 distinct leaflets, or the upper cauline ones once-ternate, petioles (1) 3–17 cm long, often with dilated, ciliate bases, blades (2) 4–11 cm long, the lateral primary leaflets about equal to the central one or a little shorter, with petiolules (0.5) 1–4 cm long, blades of leaflets 1–4 (5.5) cm long, elliptic to ovate, lobed to cleft and toothed, ciliate and often pubescent on nerves below and sometimes scattered pubescent between nerves; peduncles 3.5–15 (22.5) cm long; umbels 3–6; involucre lacking, or rarely of a solitary bract to 12 mm long; rays 3–5, 1.5–8.5 cm long, spreading to divaricate, involucels lacking or infrequently of 1 or 2 separate ciliolate bractlets to 3 mm long; pedicels 5–20 mm long, spreading to divaricate; petals greenish white; styles about 0.2 mm long; fruit, including the tails (11), 13–18 mm long, linear-clavate, the beak convex-obtuse. Oak, maple, aspen, ponderosa pine, Douglas-fir, lodgepole pine, spruce-fir, riparian, and rarely pinyon-juniper and sagebrush communities at 1,980 to 3,200 m in all Utah counties except Cache, Davis, Emery, Morgan, Piute, Rich, and Wayne; Alaska to California, east to South Dakota and New Mexico, also in the Great Lakes Region, also Chile and Argentina; 110 (xv). Very much like *O. chilensis* but generally at higher elevations and with more widely spreading rays and pedicels and shorter fruits, and much more common and widespread in Utah than is *O. chilensis*. Although the two taxa are similar and have about the same distribution in North and South America, the differences seem quite constant.

***Osmorhiza occidentalis* (Nutt.) Torr.** Western Sweet-cicely. [*Glycosma occidentalis* Nutt. ex T. & G.]. Plants 6–13 dm tall, from a taproot, with few or no persisting leaf-bases; strongly aromatic, leaves (1)2 times pinnate or the upper cauline ones ternate pinnately compound, with 3–4 pairs of opposite lateral primary leaflets, petioles of lower leaves 4–30 cm long or longer, the upper ones reduced, lower blades to 25 cm long or longer, the upper ones much reduced, the lowest pair of primary leaflets usually again pinnate, usually over 1/2 as long as the leaf blade, with petiolules 1–3.5 cm long, ultimate leaflets 1–9 cm long 0.5–4 cm wide, lanceolate to lance-elliptic or ovate coarsely toothed and some often lobed; peduncles 6–20 cm long; umbels about 3–5; involucre lacking or occasionally of 1–2 linear or filiform bracts to 16 mm long; rays 7–13, 2–6.5 cm long, involucels lacking; pedicels 2–7 mm long, calyx obsolete; petals greenish white or greenish yellow, about 1–2 mm long; stylopodium low; styles about 0.75–1 mm long; carpophore divided to the base; fruit 16–20 mm long, 2–3 mm wide, linear, glabrous. Tall forb, aspen, oak-maple, spruce-fir, riparian, and infrequently in sagebrush communities at 1,765 to 3,170 m in Box Elder, Cache, Carbon, Duchesne, Iron, Juab, Millard, Morgan, Salt Lake, San Juan, Sanpete, Sevier, Summit, Tooele, Utah, Wasatch, Washington, and Weber counties; southern British Columbia and Alberta south to California and Colorado; 67 (xvi).

Oxypolis Raf.

Perennial, caulescent, glabrous herbs from fascicled tuberous roots; leaves pinnate; umbels compound; involucre and involucel lacking; rays ascending; calyx teeth conspicuous; petals white to purple; stylopodium conic; carpophore divided to the base; fruit oblong to oval, strongly flattened dorsally, dorsal ribs filiform, lateral ribs broadly winged.

Oxypolis fendleri **(Gray) Heller** [*Archemora fendleri* Gray]. Plants 6–8 dm tall, without persisting leaf-bases; leaves pinnate with 2–5 pairs of opposite lateral leaflets, the upper ones sometimes reduced to bladeless or nearly bladeless sheaths, the petioles (3) 5–15 cm long or the upper blades sessile on a dilated sheath, blades 7–17 cm long, oblong in outline, leaflets sessile, 2–5 cm long, ovate to orbicular, shallowly to deeply crenate-dentate or serrate or rarely incised, or those of the upper leaves lanceolate to linear and sometimes entire; peduncles (1) 4–20 cm long; umbels usually 4 or more per stem; involucre lacking; rays 5–14, 1–5 (7) cm long, ascending; involucels lacking; pedicels 3–10 mm long; petals and stamens white; styles mostly less than 1 mm long; fruit 3–5 mm long. Streambanks, on Abajo and La Sal mountains in San Juan County; Wyoming south to New Mexico; 4 (0).

Pastinaca L.

Biennial or perennial caulescent herbs from large taproots; leaves pinnately compound, with broad-toothed to pinnatifid leaflets; umbels compound; involucre and involucel usually lacking; calyx teeth obsolete; petals yellow or red; stylopodium depressed-conic; carpophore divided to the base; fruit elliptic to obovate, strongly flattened dorsally, the dorsal ribs filiform, the lateral ones narrowly winged.

Pastinaca sativa **L.** Parsnip. Biennial caulescent aromatic herbs 8–15 dm tall, from a taproot; leaves pinnate or partly bipinnate in some of the lower leaflets, with 3–6 opposite or offset pairs of lateral leaflets; petioles 3–15 mm long or lacking and the blade sessile on a dilated sheath; blades 12–35 cm long or longer, oblong in outline; leaflets sessile and sometimes confluent or the lower ones sometimes on petiolules to 1.7 cm long, the blades 2.5–12 cm long, lanceolate to ovate, coarsely serrate, and often lobed; umbels 6–15 or more, the terminal one sessile or pedunculate but shorter than the 2 immediately lateral ones, the lateral umbels alternate or opposite or on opposite branches supporting 2 or more umbels; involucre lacking or of 1–few linear entire or occasionally toothed or lobed bracts to 2 (4) cm long; rays 9–25, 0.8–8.5 cm long; involucels lacking or infrequently of 1–2 linear bractlets to 2 mm long; pedicels 4–20 mm long; petals greenish yellow or reddish; styles less than 0.5 to about 1 mm long; fruit 5–8 mm long, 3–6 mm wide, broadly elliptic to orbicular or obovate, strongly flattened dorsally the dorsal ribs filiform, lateral ribs slightly winged. Ditch banks, roadsides, fence lines, gardens, fields, margins of ponds and lakes, and moist floodplains at 1,370 to 2,365 m, probably cultivated in all counties of the state, escaping and persisting, introduced from Europe, now widely established in North America; 23 (x). The cultivated plants (ssp. *sativa*) differ from the wild plants [ssp. *sylvestris*

(Mill.) Roua & Camus] in having larger roots. Some of the wild plants might be recent escapes from cultivation.

Perideridia Reichenb.

Perennial, caulescent herbs from a fusiform or tuberous root or fascicle of tuberous roots, these often deep-seated and easily detached from the rather fragile etiolated subterranean portion of the stem and often lacking in herbarium specimens; leaves ternate, pinnate, or ternate-pinnately compound, the upper ones sometimes reduced to a simple, linear rachis; petioles sheathing; umbels compound; involucre lacking or of mostly few more or less scarious bracts; involucel lacking or of 1–few bractlets; calyx teeth inconspicuous, of the texture and color of the petals (in ours); petals white when fresh; stamen white; stylopodium conic or low conic; carpophore divided to the base; fruit linear-oblong to orbicular, scarcely compressed or lightly so at right angles to the commissure, with filiform ribs.

1. Bractlets of the involucel scarious, as wide or to 5 times as wide as the pedicels, 3–5 mm long, linear to ovate, often caudate; styles 1–2 mm long after anthesis; longest rays rarely over 2 cm long; lower leaves mostly ternate-pinnately 2 or more times compound with petiolulate primary leaflets, the ultimate divisions commonly 10–50 or more per leaf .... *P. bolanderi*

— Bractlets of the involucel not scarious or with narrow scarious margins, only about as wide as the pedicels, to 3 mm long, linear or linear subulate; styles to about 1 mm long after anthesis; longest rays commonly 2–3(4) cm long; leaves ternate or pinnate; leaflets or pinnatifid divisions sessile, simple, commonly 3–5, rarely over 10 per leaf .... *P. gairdneri*

Perideridia bolanderi **(Gray) Nels. & Macbr.** Yampah. [*Podosciadium bolanderi* Gray]. Plants 23–40 cm tall, glabrous, without long-persisting leaf bases; leaves often crowded on the lower part of the stem, ternate-pinnately 2 or more times compound, with petiolulate primary leaflets, the upper ones reduced, and sometimes simple and linear, often withered before or shortly after anthesis, petioles to 4 cm long or lacking and the petiolules arising directly from a dilated sheath, blades 4–12 cm long, the ultimate leaflets strongly dimorphic, 0.2–8 cm long, mostly 10–50 or more per leaf on the lower leaves; peduncles (2) 5–14 cm long; umbels 2–6 per stem; involucre lacking or usually of 1–4 scarious bracts to 5 mm long; rays 4–12, 1–2 cm long; bractlets of the involucels about 4–8, 3–5 mm long, to 2.5 mm wide, linear to ovate and often caudate, with pale yellow-green midrib, this often flanked on either side by purple and then by conspicuous scarious margins; pedicels 3–6 mm long; petals white; styles 1–2 mm long, spreading to recurved; fruit 3–4 (5) mm long, some of the ribs usually conspicuously ridged. Sagebrush, juniper, mountain brush, and stream-side communities, sometimes in snowflush areas at 1,524 to 2,320 m in the western 1/2 of Box Elder County and Deep Creek Mountains., Juab County; eastern Oregon and western Idaho south to California and Utah; 12 (iii). Sometimes confused with *P. gairdneri*, but in addition to the several features listed in the key it differs as follows (features of *P. gairdneri* in parentheses): peduncles mostly 5–14 cm long (mostly 1–5 cm long); fruit 3–5 mm long, oblong, the ribs ridged (2–3 mm long, orbicular, the ribs obscure).

Perideridia gairdneri **(H. & A.) Mathias** False Yarrow [*Atenia gairdneri* H. & A.; *Carum garrettii* A. Nels. in Coult. & Rose, type from the Wasatch Mountains]. Plants 15–75 cm tall, glabrous, without long-persisting leaf bases; leaves 2–5 per stem, ternate or pinnate, with up to about 5, rarely more, sessile leaflets, the upper ones reduced and often simple and linear; leaflets to 13 cm long, mostly confluent with the rachis, linear and hardly wider than the petiole, occasionally expanded to 11 mm wide; peduncles (1) 2–5 (7) cm long; umbels 2–5 per stem; involucre lacking or occasionally of 1 or 2 linear bracts to 6 mm long; rays 7–16, 0.7–4 cm long; bractlets of the involucels lacking or more often 1–6, 1–3 mm long, linear or linear-subulate, hardly if at all wider and conspicuously shorter than the pedicels, not marked with purple or if so then the whole bractlet mostly purple; pedicels 3–5 mm long; petals white or turning purplish; styles to 1 mm long, recurved; fruit 2–3 mm long, orbicular, the ribs obscure. Sagebrush, forb-grass-silver sagebrush, meadow, oak, maple, aspen, and willow-streamside communities at 1,680 to 2,685 m in eastern Box Elder, Cache, Daggett, Juab, Salt Lake, Sanpete, Summit, Utah, and Wasatch counties; British Columbia to southern California, east to Saskatchewan and New Mexico; 25 (v). Our plants belong to ssp. *borealis* Chuang & Const.

Podistera Wats.

Perennial acaulescent glabrous plants from taproots or branched caudices; leaves pinnate with deeply lobed leaflets; umbel solitary, compound, compact; involucre wanting; involucel of toothed bractlets; calyx teeth conspicuous, ovate; petals greenish yellow; stylopodium conic; carpophore stout, undivided; fruit oval, slightly flattened laterally, the ribs filiform to prominent.

Podistera eastwoodiae **(Coult. & Rose) Mathias & Const.** [*Ligusticum eastwoodae* Coult. & Rose]. Plants 7–20 (30) cm tall, acaulescent, without or with few long-persisting leaf bases; leaves pinnate, with 4–6 pairs of sessile lateral leaflets, petioles 1.5–7 cm long; blades 2.5–7.5 cm long, oblong in outline; leaflets about 1–2 cm long, ovate to obovate in outline, ternately or palmately lobed or cleft, the larger lobes again toothed or lobed; peduncles (7) 10–20 (30) cm tall; involucre lacking; rays 5–8, 2–8 mm long; bractlets of the involucel 4–6 mm long, often exceeding the flowers and fruit, ovate or obovate, with 2–3 teeth or lobes, with the texture and color of the leaves; pedicels 1–2 mm long; petals greenish yellow, turning purple; styles about 1 mm long; fruit about 3–4 mm long, the ribs evident but not winged. Apparently rare at upper elevations of the La Sal Mountains, San Juan County; Colorado, New Mexico, and Utah; 0 (0).

Sium L.

Perennial, caulescent herbs from fascicles of fibrous roots; leaves mostly pinnately compound or decompound, with well-marked, toothed to pinnatifid leaflets; umbels compound; involucre of entire or incised, often reflexed bracts; involucel of narrow bractlets; calyx teeth minute or obsolete; petals white, stylopodium depressed or rarely conic; carpophore divided to the base (but threadlike and adnate to the faces of the mericarps in our plants); fruit elliptic to orbicular, slightly compressed laterally and somewhat constricted at the commissure, the subequal ribs prominent and corky but hardly winged.

Sium suave **Walt.** Hemlock Water-parsnip. Plants 5–10 dm tall; leaves pinnate or occasionally partly bipinnate, with 4–6 opposite pairs of sessile lateral leaflets, lower petioles to 25 cm long, often septate, the upper ones smaller and sometimes reduced to a dilated sheath, lower blades 14–32 cm long, the upper ones reduced; leaflets 2–8(15) cm long, (1) 3–8 (20) mm wide, linear to lanceolate, sharply and uniformly serrate to pinnatifid with linear segments; peduncles 4–10 cm long; umbels 3–11 or more per stem; involucre of about 1–6 separate, often reflexed bracts 2–9 mm long; rays 11–24, 1.5–3 cm long; involucels of (2) 5–12 separate bractlets 2–5 mm long; pedicels 2–8 mm long; petals and stamens white; styles about 1 mm long; fruit 2–3 mm long, the ribs prominent. Mud flats, marshlands, wet meadows, along streams and shorelines, and in ponds and lakes at 1,365 to 2,990 m in Garfield, Piute, Rich, Salt Lake, Sanpete, Sevier, Utah, and Wayne counties; southern British Columbia to Newfoundland, south to California and Virginia; 15 (i). Often confused with *Cicuta* and frequently found with that genus in herbaria, but conspicuously different by the merely pinnate leaves.

Torilis Adans.

Annual caulescent hispid or pubescent herbs from slender taproots; leaves 1–2 times pinnate or pinnately decompound, petioles sheathing; umbels compound, capitate or open, sessile or pedunculate; involucre lacking or of a few small bracts; involucel of several linear or filiform bractlets; calyx teeth evident to obsolete; petals white; stylopodium thick, conic; carpophore bifid or cleft ca 1/3–1/2 its length; fruit ovoid or oblong, flattened laterally, tuberculate or prickly, the primary ribs filiform, setulose, the lateral ribs displaced onto the commissural surface, the intervals covered with glochidiate prickles or tubercles.

Torilis arvensis **(Huds.) Link** Hedge Parsley. [*Caucalis arvensis* Huds.]. Plants 3–10 dm tall, divaricately branched, appressed-hispid throughout, retrorsely so on the stems and antrorsely so on the leaves and rays; leaves 2–3 times pinnate, or the upper ones once-pinnate, the ultimate leaflets 5–60 mm long, 2–20 mm wide, ovate to linear lanceolate, acute or acuminate, regularly incised or divided; peduncles 2–12 cm long; involucre lacking or of a single small bract; rays 2–10, 0.5–2.5 cm long; involucel of several subulate bractlets longer than the pedicels; pedicels 1–4 mm long; petals white; styles short; fruit ovoid-oblong, 3–5 mm long, the mericarps densely covered with straight glochidiate prickles with minute retrorse-barbs, these spreading almost at right angles and about as long as the fruit is wide. LaVerkin in orchard, (Barnum 1316 BRY); Washington County; adventive; introduced from southern and central Europe; 1(0).

Yabea K.-Pol.

Annual caulescent herbs from taproots; leaves pinnate or dissected; umbels compound; involucre of a few entire or dissected, usually somewhat scarious bractlets; calyx teeth evident; petals white; stylopodium thick and conic; carpophore entire or bifid at the apex; fruit oblong or ovoid, somewhat compressed laterally, with spreading uncinate prickles along alternating ribs, and bristly-hairy on the other ribs.

***Yabea microcarpa* (H. & A.) K.-Pol.** California Hedge-parsley. (*Caulis microcarpa* H. & A.). Plants annual, caulescent, 8–40 cm tall, pubescent with spreading hispid hairs, from a slender taproot; leaves 2–3(4) times pinnate or ternate-pinnate, with about 3–4 opposite pairs of lateral primary leaflets, blades 1–5 cm long, oblong or ovate in outline, on petioles 1–4.5 cm long or the upper ones sessile, lowest pair of primary leaflets about 1/2 as long as the leaf blade, sessile or petiolulate, ultimate segments 1–8 mm long, 0.5–2 mm wide; peduncles 3–10 cm long; umbels 1–4, involucre resembling the upper leaves or a little smaller; rays (1) 2–7 (9), 1.5–10 cm long, often about as long as the peduncles; involucels similar to the involucre, but usually reduced, sometimes much reduced and the bractlets only pinnatifid or entire; pedicels 5–15 cm long; petals white; stamens white; styles very short; carpophore bifid for about 1/5 its length; fruit 3–7 mm long. The one specimen seen (Atwood 4871 BRY) is from the Pine Valley Mountains, Washington County; British Columbia south to Baja California, east to Idaho and Arizona; 1(0).

Zizia Koch

Perennial glabrous or subglabrous herbs with basal and cauline leaves, from a short caudex and a cluster of fleshy-fibrous roots; leaves simple or ternate, with toothed blades or leaflets; umbels compound; involucre lacking or obsolete; involucel of a few inconspicuous bractlets; calyx teeth well developed; petals bright yellow; stylopodium lacking; carpophore bifid about 1/2 its length; fruit oblong or broadly elliptic, somewhat laterally compressed, the ribs prominent but not winged.

***Zizia aptera* (Gray) Fern.** [*Thaspium trifoliatum* var. *apterum* Gray]. Perennial, caulescent, glabrous herbs 15–50 cm tall, from a taproot or fascicle of roots, without long-persisting leaf bases; basal leaves simple, rarely ternate, petioles 3–18 cm long, blades 1.5–5 cm long, ovate to nearly orbicular, cordate, crenate-serrate; cauline leaves ternate, not over 3 cm long, the leaflets sessile or on petiolules to 4 mm long; peduncles 6–12 cm long; umbels 1 or 2 per stem; involucre lacking or obsolete; rays 10–17, 0.5–2 cm long; involucels of about 4–6 bractlets, to about 2 mm long, separate or united at the base; pedicels 1–3 mm long; petals yellow; stamens yellow; styles about 1 mm long; fruit about 2 mm long, the ribs prominent. Willow-streamside and meadow communities at 2,130 to 2,440 m in Sanpete, Sevier, Summit, Utah, and Wasatch counties; widespread in the United States and Canada; 12 (iii).

QUERCUS (FAGACEAE) IN THE UTAH FLORA

Stanley L. Welsh[1]

ABSTRACT.—Reviewed are the oak taxa as they are presently understood in Utah. Keys and descriptions are included, occurrences are cited, and problems of hybridization are discussed. Named as new varieties from Utah are *Quercus gambelii* Nutt. var. *bonina* Welsh and *Quercus havardii* Rydb. var. *tuckeri* Welsh. Both varieties occur in southeastern Utah. *Quercus eastwoodiae* Rydb. is proposed as a hybrid.

The native oaks have been a source of confusion almost from the beginning of botanical exploration, and a huge bibliography has accumulated dealing with the oaks of Utah and the West (Harper et al. 1985). Collection of the materials serving in typification of the earliest known portion of the complex of species existing in Utah confounded interpretation from the beginning. The first epithet in our oaks and a name that has long plagued Utah plant taxonomy, *Quercus undulata* Torr., was published in 1828 and is based on material taken by Dr. James on the Long Expedition in the summer of 1820 (Tucker 1971). The exact nature of the type material has remained obscure for reasons reviewed by Tucker (1971), but the material was evidently taken in Harding County, New Mexico, a place where *Q. gambelii* Nutt. and *Q. grisea* Liebm. coexist. Although indicating that "the type shows scant evidence of the influence of *Q. gambelii* (aside from characters of foliar trichomes)," Tucker (1971) concludes that the locality from which the type was taken contains a mixture of intermediates between the parental taxa and that the "'species'—*Quercus undulata*— is in fact a variable complex derived from hybridization." The observations made by Tucker suggest, however, quite a different application of the name, i.e., that it should replace *Q. grisea*, a later synonym. Interpretation of the type specimen, not the population that it came from, is crucial in typification. The cloud still remains, but fortunately it is beyond the bounds of Utah.

The Utah oaks belong to three main population complexes: *Q. gambelii* Nutt., *Q. turbinella* Greene, and *Q. havardii* Rydb. Within those complexes the species concepts are mostly clear and unarguable, but they have no really apparent barriers to hybridization, and intermediates are known between nearly all of them.

The following taxonomic treatment is based on the examination of more than 300 specimens in Utah herbaria and more than three decades of experience with oaks in the field.

Numbers following the descriptions of the taxa and hybrids indicate the number examined (in Arabic numerals) and the number collected by me (in Roman numerals).

Quercus L.

Trees or shrubs; wood hard, ring-porous, with prominent rays; leaves alternate, lobed, toothed, or entire; staminate flowers in usually pendulous, naked catkins; bracts caducous; calyx with 2–8 lobes; stamens 3–12; pistillate flowers with a subtrilocular, 6-ovuled ovary; stigma 3-lobed, enclosed by a scaly involucre, this hardened and cuplike, surrounding the base of the nut or acorn.

1. Leaves evergreen, the lobes of teeth spinescent, or seldom entire; plants of Washington, and, less commonly, of Kane and San Juan counties, hybridizing with the following .... *Q. turbinella*

— Leaves deciduous (persistent in some hybrids), the lobes variously angled or rounded, but seldom, if ever, spinescent; plants of broad or other distribution...................... 2

2(1). Leaf lobes typically 1–2 times longer than the width of the leaf axis, rounded to obtuse or less commonly acute and often bilobed apically; plants broadly distributed .... *Q. gambelii*

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— Leaf lobes seldom, if ever, as long as the width of the leaf axis, acute to acuminate apically 3

4(3). Plants deciduous, colonial in sandy sites, typically with branch ends protruding above the substrate 1–5 dm; acorns mostly over 15 mm long and about as broad; hybridizing with the former along canyons . . . . *Q. havardii*

— Plants semievergreen, mainly 10–30 dm tall or more, or, if deciduous, the leaves typically hairy above and densely so beneath, forming clones within and adjacent to stands of *Q. gambelii*, and occurring sporadically where *Q. gambelii* and *Q. turbinella* or *Q. havardii* coexist; acorns typically less than 15 mm long and less than 10 mm wide, if formed at all . . . . *Q. pauciloba* and *Q. eastwoodiae* (hybrids)

***Quercus gambelii* Nutt.** [*Q. stellata* var. *utahensis* A. DC., type from west of Salt Lake City (?); *Q. utahensis* (A. DC.) Rydb.]. Clonal, deciduous shrubs or small trees, or less commonly trees to 10 m tall and with a trunk diameter to 6 dm or more thick, spreading by rhizomes; leaves densely grayish or yellowish stellate hairy on both surfaces when young, in age stellate hairy and paler beneath but glabrate and green and subglossy above, 2.4–17 cm long, 1–11 cm wide, obovate to elliptic in outline, the sinuses obliquely descending about 1/4–3/4 to the midrib, the lateral lobes (0) 2–10, oblong to lance-oblong, entire or notched apically and sometimes again laterally; staminate catkins 3.5–5 cm long; involucral cup 3–10 mm long, 10–17 mm wide, short-pedunculate to subsessile, ca 1/4–1/2 the length of the acorn, clothed with imbricate, densely hairy scales; acorns 8–18 mm long, 7–15 mm thick. Mountain brush, sagebrush, pinyon-juniper, ponderosa pine, and aspen communities at 1,125 to 2,745 m in all Utah counties except Daggett and Rich (?); Wyoming, Colorado, New Mexico, Arizona, Nevada, Texas, and Mexico; 206 (xxi).

Gambel oak is central to a series of problematical taxa, belonging in a broad sense to the *Q. undulata* Torr. complex, in which every degree of consanguinity is recognized. All our indigenous oaks are portions of the complex, and all form intermediates wherever contact is or has been made. Viewed broadly, all could be regarded as phases of *Q. undulata*, sensu latissimo. Problems related to such an approach involve similar circumstances of hybridization with species belonging to other oak groups away from the *Q. undulatum* centrum. Ultimate consolidation of all intergrading groups would lead to absurdity. There is one variant within *Q. gambelii*, however, that is so different as to require taxonomic recognition, as follows: **Var. *bonina* Welsh** var. nov. Persimilis *Querco gambelii* var. *gambelii* in foliis et habitu sed in glandibus (27–33 mm longis nec 8–18) et cupulis (20–25 mm latis nec 10–17) majoribus differt. Type: USA: Utah. San Juan County, T36S, R13E, S28, GCNRA, Lake Powell, Goodhope Bay springs, Cottonwood, oak, willow community, sandy alluvium over Chinle Formation, 21 Sept. 1983, S. L. Welsh & E. Neese 22575 (Holotype BRY; 6 isotypes distributed previously as *Quercus*). The Goodhope oak clusters about several springs on the east side of Goodhope Bay in the Glen Canyon National Recreation area. One of the stands has been burned by negligent recreationists, but all bear the large acorns atypical of *Q. gambelii* from other sites. Seeds taken at the time of the original collection were grown in the greenhouse at Brigham Young University by Mr. Tom Black, who planted them simultaneously with others of *Q. gambelii* from Utah County. By May of the year following, the seedlings of the Goodhope oak were twice as large as those from Utah County. The plants at Goodhope Bay tend to average larger than those from other localities along Glen Canyon, but they do not appear to differ otherwise. The size might be a function of the continuous water supply available in the spring and seep areas. The spring area seems to be associated with joint systems in the Wingate Formation to the east, these allowing water to penetrate to the impervious Chinle Formation, where the water surfaces.

***Quercus havardii* Rydberg.** Shinnery Oak. [*Q. undulata* authors, not Torr.]. Clonal, deciduous, sand-binding shrubs, or, less commonly, small trees to 2 m or more; leaves densely grayish to yellowish stellate-hairy on both sides when young, less densely so in age, but only slightly, if at all, paler beneath than above, even in age, 1.5–5.5 cm long, 0.9–3.3 cm wide, oblanceolate to elliptic in outline, with usually 6–10 toothlike lateral lobes, these typically apiculate-acuminate and sometimes further notched or toothed apically; catkins 1–2.5 cm long; involucral cups 7–10 mm long, 14–18 mm wide, subsessile, ca

1/4–1/3 the length of the acorn, clothed with imbricate, densely hairy scales; acorns 15–23 mm long, 14–18 mm thick. Blackbrush, ephedra, vanclevea, purple sage, and pinyon-juniper communities, usually in sand, at 1,125 to 2,135 m in Emery, Garfield, Grand, Kane, San Juan, and Wayne counties; Arizona, New Mexico, Oklahoma, and Texas; 54 (x). The shinnery oak, as it occurs in Utah and adjacent Arizona, is more or less influenced by intergradation with the partially sympatric *Q. gambelii* and *Q. turbinella* (Tucker 1970). Intermediates between both of those parental types and *Q. havardii* are known. However, in the sandy footslope of the San Rafael Swell in Emery and Wayne counties and adjacent portions of the Navajo Basin of Utah and Arizona, the species is more or less stable and tends to be habitat specific.

Possibly because of the contribution of both *Q. gambelii* and *Q. turbinella*, even the more uniform portions of the species differ from the body of the taxon lying far to the east in New Mexico, Texas, and Oklahoma. The Navajo Basin material differs from the parental type in smaller and more densely hairy leaves that tend to be sharply toothed. Because of the differences noted and because of the isolation of the Navajo Basin material from its eastern counterpart, our material is regarded as **Var. *tuckeri* Welsh** var. nov. Planta inter *Querco gambelii* Nutt. et *Q. turbinella* Greene et *Q. havardii* Rydb. var. *havardii* sed in pro max parte *Q. harvardii* Rydb. var. *harvardii* maxime affini, sed in foliis minoribus et pilis plus dense, et dentibus acutis differt. TYPE: USA: Utah. San Juan Co., Low Pass, ca 8 mi SE of Moab, T27S, R23E, S.5, mixed desert shrub community, Entrada Sandstone Formation, at 1,635 m, 10 July 1985, S.L. Welsh and L. C. Higgins 23630 (Holotype BRY; Isotypes to be distributed). Additional specimens: Utah, San Juan County, Elephant Hill vicinity, in pinyon-juniper community, Canyonlands National Park, 6 May 1969, S. L. Welsh, D. Atwood, & L. Higgins 8878 (staminate, BRY); Garfield Co., Henry Mts., 5 May 1977, E. Neese & S. White 2784. Grand Co., Moab, 8 June 1927, W. P. Cottam, 2139; Courthouse Towers, 25 Apr 1947, B. F. Harrison 11124; Arches National Park, 2 ,May 1963, L. B. Barnett et al. 56, 66; 13 July 1972, J. S. Allan 128; 19 July 1972, J. S. Alan 133; 5 mi NW of Moab, 21 May 1984, D. Atwood et al. 9699. Kane Co., 28 mi e of Kanab, 11 May 1953, B. F. Harrison 12049; 60 mi SE of Escalante, 7 Aug. 1957, B. F. Harrison 12723; Dance Hall Rock, 2 May 1962, J. R. Murdock 381; Hole-in-the-Rock, 4 May 1962, D. A. White 125, 27 Apr 1977, R. Foster 3602; Escalante Arm of Lake Powell, 5 June 1927, S. L. Welsh & G. Moore 11825, 11826. San Juan Co., Bluff, 2 July 1927, W. P. Cottam 2529, 2532; Monument Valley, 4 July 1927, W. P. Cottam & S. Hutchings 2585; Cow Canyon, 29 Apr 1961, C. A. Hansen 97; Squaw Flat, 15 May 1965, G. Moore 375. All are deposited at BRY.

***Quercus pauciloba* Rydb.** (hybrid) Clonal, semievergreen shrubs or small trees mainly 2–4 m tall and with trunks 4–15 cm in diameter; leaves stellate-hairy on both surfaces when young, becoming sparingly so to glabrate on one or both sides in age, bicolored (more or less), typically green to dark green above and paler beneath, 2–10 cm long, 1–7 cm wide, usually with (0) 4–8 toothlike lateral lobes, these typically apiculate and sometimes apiculate-acuminate, rarely some of them again notched or toothed; staminate catkins 3–4 cm long; pistillate catkins, mature involucral cups, and mature acorns not present in specimens examined. Sagebrush, mountain brush, pinyon-juniper, and ponderosa pine communities at 1,220 to 2,045 m in Beaver, Iron, Juab, Kane, Millard, Salt Lake, Tooele, Utah, Washington, and Weber counties; Colorado, Arizona, and Nevada; 11 (0). Specimens designated as *Q. pauciloba* consist of an aggregation of hybrids and presumed introgressants involving *Q. gambelii* and *Q. turbinella* as parental types. They occur relatively commonly in areas where the two parental species coexist in Washington and Kane counties, but they occur also along the western margin of the plateaus and mountains north to Weber County, far removed from the body of *Q. turbinella* in Washington, Kane, and San Juan counties. The hybrids and introgressants are about on a line marking the edge of the major overthrust fault that bisects Utah. Cottam et al. (1959) and Tucker (1961a, 1961b, 1970) have postulated an interglacial advance of *Q. turbinella* into the Great Basin, followed by a retreat during return of harsh conditions. The hybrids were presumed to represent first generation only, were postulated to have resulted during the incursion, and were judged to have persisted following the retreat of the one parental type. Ruled out are other possibilities such as long-distance pollination, suggested as a probability by Harper et al. (1985) and concurred in by me, because of lack of coincidence of flowering times, primarily.

Examination of specimens of the hybrid complex demonstrates several problems. First, the variation among the intermediates is greater than would be expected from first generation hybrids, suggesting introgression as well as hybridity. Indeed, a specimen from the mouth of American Fork Canyon (Lindquist s.n. 20 Jan 1981 BRY) is strictly evergreen, has staminate catkins and abortive acorns, and, if placed within specimens of *Q. turbinella* from Washington County, would be identified as that species. Second, although mature acorns and caps were not noted on the specimens examined, staminate catkins were present in some, suggesting the possibility of introgression occurring far north of the primary pollen source. And, the following questions are unanswered by the flow and ebb hypothesis: (1) Did a migration route occur during the time of the thermal maximum that is not now in evidence? (2) Was not a simpler and as equally accessible a route available along the canyons of the Colorado (where *Q. turbinella* exists in some small part, even now) and, if so, where is the matching set of hybrids in the Colorado Basin? (3) Could not long-distance pollination, even though the juxtaposition of flowering time occurs only irregularly, be sufficient to account for some, if not all, of the occurrences of the hybridization northward? And does not the pattern of distribution of hybrids along the windward side of the Wasatch frontal ranges suggest long-distance pollination? Additional studies are indicated.

***Quercus eastwoodiae* Rydb.** (hybrid) In the Navajo Basin of Utah, along the Colorado River and its canyons, another set of hybrids and presumed introgressants are known. In general aspect and leaf morphology they resemble *Q. pauciloba*, but their origin seems to be different. Gambel oak grows at even the lowermost elevations in mesic canyons, on stream terraces, and around seeps, springs, and hanging gardens. Although *Q. turbinella* is present also, the extent and total numbers appear to be limited now, and there does not seem to be evidence of a much greater incidence in the past. The turbinella live-oak is present at the confluence of Glen Canyon and the San Juan River, and also occurs as a narrow tongue along the Cockscomb in central Kane County, where it is confluent southward into the Houserock Valley area of Arizona. Intermediates between turbinella live-oak and Gambel oak are also known from this latter region.

In the remainder of the Navajo Basin the picture is complicated by still another *Quercus* species, i.e., the shinnery oak, *Q. havardii*. That species occurs as a moderately stable entity on the sandy plateaus and slopes away from the canyons proper but reaches to their margins, where the stream courses are deeply entrenched. They, too, hybridize with Gambel oak, and the hybrids and presumed introgressants survive in usually sheltered positions adjacent to or intermixed with Gambel Oak. Such intermediates are known also from the islandlike mountains that protrude from the floor of the Navajo Basin. Intermediate specimens appear superficially like those of *Q. pauciloba*, but they tend to be more densely hairy, to have hairs persistent on the upper surface, even in age, and to be less distinctly green, even if bicolored. These intermediates are here designated as *Q.* x *eastwoodiae* Rydb. (Bull. New York Bot. Gard. 2: 210. 1901; based on, Eastwood 141, from Butler Wash, San Juan County, Utah in 1895), although the description of the type specimen indicates it to be a portion of the variation nearer to *Q. gambelii*. The plants are present in blackbrush, other warm-desert shrub, mountain brush, pinyon-juniper, and Douglas-fir communities at 1,130 to 1,830 m in Garfield, Grand, Kane, and San Juan counties; Arizona; 13 (ii).

***Quercus turbinella* Greene** Turbinella Live-oak. Clump-forming (clonal?) evergreen shrubs or, less commonly, small trees, mainly 1–4 dm tall and with stem diameters to 2 dm; leaves yellowish stellate-hairy on both surfaces when young, finally glabrate and glaucous above, not especially bicolored, typically 1.3–4 cm long, 0.7–2.4 cm wide, lanceolate to oblong or suborbicular in outline, with 2–6 pairs of lateral, spine-tipped teeth or entire; staminate catkins 1–3 cm long; involucral cup 6–8 mm long, 10–14 mm wide, ca 1/4 as long as the acorn; acorns 12–24 mm long, 7–10 mm thick. Chaparral (oak, manzanita, ceanothus), pinyon-juniper, and riparian communities at 820 to 1,710 m in Kane, San Juan, and Washington counties; Nevada and Arizona; 39 (iv).

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SEASONAL PHENOLOGY AND POSSIBLE MIGRATION OF THE MOURNING CLOAK BUTTERFLY *NYMPHALIS ANTIOPA* (LEPIDOPTERA: NYMPHALIDAE) IN CALIFORNIA

Arthur M. Shapiro[1]

ABSTRACT.—Circumstantial evidence is presented that suggests the Mourning Cloak undergoes regular seasonal up- and downslope movements in northern California. The species breeds at low elevations in spring and then disappears until autumn; its disappearance coincides with the appearance of fresh individuals in the Sierra Nevada alongside obvious hibernators.

The Mourning Cloak or Camberwell Beauty, *Nymphalis antiopa* L., is one of the most characteristic Holarctic butterflies; it ranges from the subarctic to the subtropics. Nonetheless, its basic biology is poorly known. There have been many discussions of its rare and intermittent occurrence in the British Isles (Williams et al. 1942, Williams 1958, Chalmers-Hunt 1977), but only one detailed description of its natural history—that by Young (1980), who narrated the situation in Wisconsin, USA, in the hope that it would help Palearctic workers understand the dynamics of their own populations. The biology of *N. antiopa* in California, USA, is quite different; specifically, it seems to involve either estivation or altitudinal migration or both. Altitudinal migration appears to occur in California populations of *N. (Aglais) milberti* Latr. and *N. californica* Bdv. (Shapiro 1973, 1974a, 1974b, 1975, 1979, 1980).

Since 1972 phenological data have been taken for all butterflies at a series of stations forming a transect parallel to Interstate Highway 80 from sea level at the Suisun Marsh, Solano County, to tree-line at Castle Peak, Nevada County (2750m). Each station is visited at roughly two-week intervals throughout the butterfly season, and all species flying are recorded. Figures 1 and 2 represent the *N. antiopa* data from this transect for 1983 and 1984. These two years were extremely different meteorologically and essentially embrace the range of variation observed during the 13 years of the study. The year 1983 was one of record high precipitation, with both rainfall and snowpack greater than 200% of the 30-year means. Summer was cool and unusually moist, after a very late and cloudy spring. Precipitation in the 1983-84 season was slightly below normal. Rain- and snowfall were heavy before Christmas and nearly nonexistent thereafter. Spring was early and hot, and summer 1984 was the hottest of record (over 125 years) at low elevations and much warmer than normal in the mountains, with an unusual frequency of thunderstorms. The fact that the seasonal patterns of *N. antiopa* are consistent in two such different years suggests that they accurately represent the seasonal dynamics of the animal.

Shapiro (1974c) reported that *N. antiopa* was univoltine in the Sacramento Valley despite the very long growing season. Nearer the coast, at the Suisun Marsh, Shapiro (1974d) reported essentially the same phenology. The same pattern was again reported for suburban Sacramento by Smith (1983). Smith provides counts of sightings at one specific locality for the years 1970 through 1982. His pattern is quite consistent, with no animals seen after 8 July in 50% or more of years, after a very dramatic peak between 20 May and 1 July. It was initially assumed by Shapiro that the single spring brood in these areas entered estivation, followed by a brief period of activity in autumn, followed by hibernation, such that Sacramento Valley animals lived a full year as adults. Although estivation remains a possibility, no estivating adult has been found

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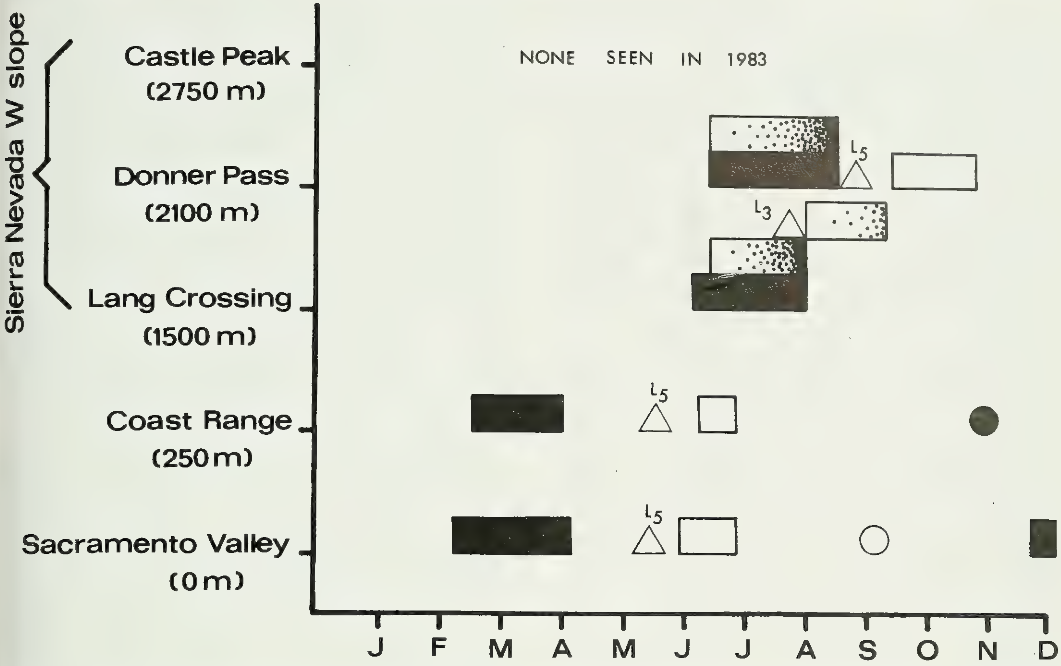

Fig. 1. Phenology of *Nymphalis antiopa* along a transect across northern California in 1983. Intensity of stippling indicates degree of wing wear. Dots are individual occurrences. Triangles are observations of larval colonies: L_3=third instar, etc.

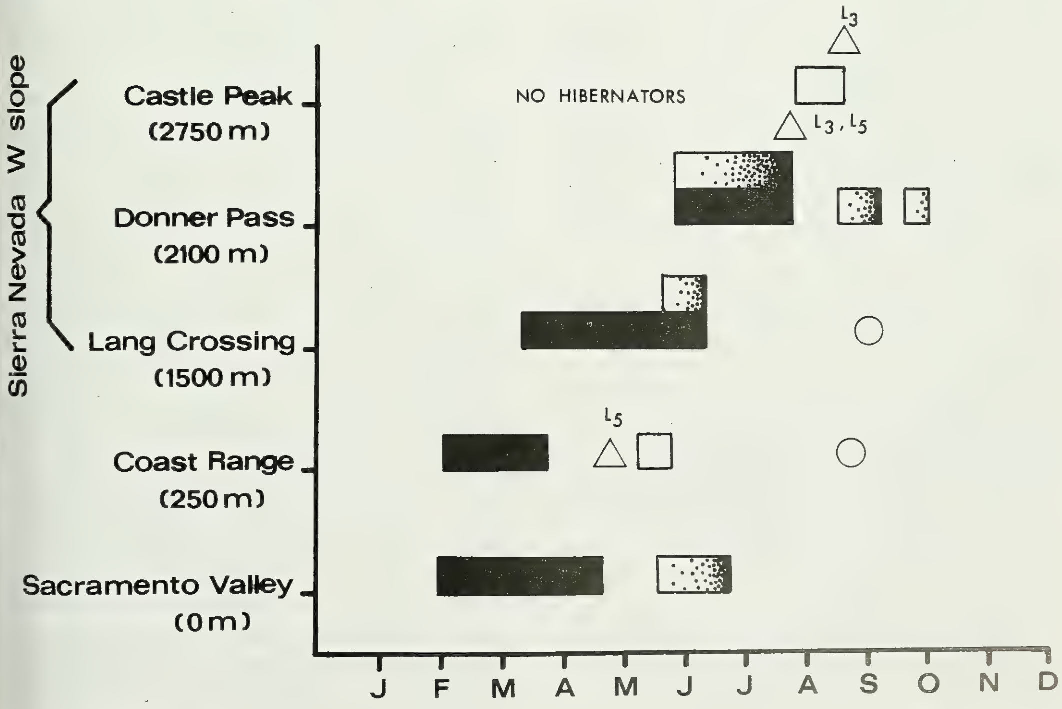

Fig. 2. Same for 1984.

in 13 years, the condition of the adults observed in autumn and early winter argues against it, and, most importantly, there is a persuasive circumstantial case implicit in Figures 1 and 2 for altitudinal migration on a regular seasonal basis.

Overwintered adults in typical posthibernation condition (borders nearly or totally white, much wing wear) were observed near Sacramento and in the Inner Coast Range beginning in late winter in both years. Similar hibernators appear at montane sites shortly after snowmelt—the timing of which varied by several weeks between the two years. The single flight of fresh animals was observed at low elevations in late May–early July, lasting from 10 to 41 days in different locations. Smith (personal communication) saw singletons in Sacramento during the second, third, and fourth (three records) weeks of July and the second week of August, 1983, and on 9 July and 25 July 1984.

As can be seen from Figures 1 and 2, at mountain stations more or less fresh animals can also be found in spring, flying with the hibernators. At Lang Crossing (1500 m), for example, the first 1984 hibernators appeared on 10 March and fresh animals followed on 6 May while hibernators were still numerous. At Donner Pass (2100 m), both fresh and worn animals were already flying 27 May and continued to be distinguishable through 20 June. Thereafter, worn animals probably derived from both groups flew until 20 July. On that date two colonies each of 3rd- and 5th-instar larvae were censused, presumably representing a differential in the timing of reproduction by the two groups of adults. On 15 August fresh adults were very numerous in the vicinity of the previous L_5 colonies. By 6 September only a few were present and these were moderately worn, but a second group of fresh animals appeared 19 September and flew for a week.

At the highest station, Castle Peak (2750 m), there is no permanent population, and the species is present in some years (generally those with early snowmelt) and absent in others (generally late years). It was absent in 1983. In 1984 no hibernators were seen, but fresh animals flew 27 July– 17 August, and on the latter date one colony of L_3 was found.

Given that reproduction by *N. antiopa* was late at low elevations in 1983 and that the timing of snowmelt was even more distorted, it is striking that in both years figured (and in general) the appearance of fresh animals at mountain stations commences about a week after the valley brood appears.

Similarly, the widely scattered autumn sightings are properly timed to represent downslope dispersal by the midsummer brood reared in the mountains. Several apparently fresh *antiopa* were seen at Lang Crossing 30 August (two weeks after the flight started at Donner; no larval colonies were seen at Lang in 1984). One apparently fresh specimen was seen in Gates Canyon in the Inner Coast Range on 26 August, and Smith saw one in Sacramento on 4 September.

Nothing in these data either requires altitudinal migration or precludes estivation, but they are clearly suggestive. How plausible is the hypothesis of altitudinal migration? One alternative explanation is that *antiopa* may over-winter in both the adult and pupal stages in the Sierra Nevada. Klots (1951) raised this possibility for the eastern United States. Shapiro (1969) recorded a single case in central New York in which overwintering of the pupa seems inescapable; the animal, when captured, voided meconium. I have tried repeatedly to maintain laboratory-reared lowland California pupae at 2–3 C for extended periods, but with no success after eight weeks. True pupal diapause appears to be unknown in the Nymphalini.

Another alternative explanation for the low-altitude phenomena is a low level of reproduction in summer. In 13 years of extensive field work in the Sacramento Valley and Inner Coast Range, I have never found a single larval colony after 1 June, nor has Smith in 14 years at Sacramento. On the other hand, second broods occur occasionally beginning at Fairfield, Solano County, nearer the coast, and even a third brood has been recorded (L_5, 20 October 1980). This is apparently standard on the immediate coast, for Tilden (1965) reports "two to three broods a year" in the San Francisco Bay area, and Emmel and Emmel (1973) report "multiple-brooded at lower elevations and single- or double-brooded in higher zones" in southern California—the "lower elevations" referring almost entirely to urban and suburban areas, not to the interior deserts. *Nymphalis antiopa* is a common urban species in Mexico City, where it breeds all year.

Some light can be shed on the annual cycle by examining the reproductive status of the animals. Although Young (1980) claims that spring populations consist solely of females—the males presumably having died overwinter—this is not true in California (or southeastern Pennsylvania or New York). In the Sacramento Valley and Coast Range, courtships and matings are observed both in autumn (occasionally) and spring (frequently). At Donner Pass they have been observed in September but not in spring. In 1984 I dissected eight August and three September Donner females. All had large amounts of fat and no well-developed oocytes, but all the August and none of the September females were virgins. All the fresh-looking females collected in the mountains in June and July have been fully reproductive (N=15).

Herman and Bennett (1975) reported that summer females (source population and rearing regime unspecified) eclose with large fat bodies and no oocytes, and subsequently mature as a function of environment. Maturation was essentially completed within 10 days at 25 C on LD 16:8 but did not occur after 14 days at 10 C, LD 8:16. This experiment does not separate the effects of photoperiod and temperature. Photoperiods at Donner Pass in late August are ca LD 13.5:10.5, mean temperature 16 C. Donner Pass *antiopa* reared on LD 14:10 at 25 C failed to mature after 15 weeks in the dark at 2 C.

For adult *antiopa* emerging in the Sacramento Valley in late May, photoperiods are ca LD 15:9 and mean temperature 18.9 C, conditions that should permit rapid gonadal maturation, but no reproduction is seen. Of three late May–early June Sacramento females, two had mated and one of these showed early oocytes. If altitudinal migration is real, ovarian maturation may occur during the upslope flight, its termination coinciding with the beginning of oviposition. The distances involved (125–150 km from our Sacramento Valley sites to Donner Pass) could be traversed in a week or so, based on the progress of *N. californica* migrations I have tracked.

Shannon (1917) believed eastern U.S. populations of *N. antiopa* were at least somewhat migratory. Gibo (1981) records the species riding thermals in east central Canada; such passive soaring is associated in many insects with the initiation of long-range dispersal.

One additional aspect of the problem deserves mention. Shapiro (1981a,b) studied the canalization of the wing pattern as a trait adaptive to climate. He found that Alaskan animals are more strongly buffered physiologically against cold shock than either lowland or Sierran montane *N. antiopa*. The similarity of the physiological responses of the Californian broods, from radically different climates, could imply gene flow over the fairly short distances separating them—an interpretation consistent with the notion of altitudinal migration. Since the 1981 papers were published, the California experiments have been replicated three times with the same results for the major aberration "hygiaea." The minor pattern differences reported in Shapiro (1981b) have been inconsistent among broods. Granted that at least part of the population of *N. antiopa* overwinters at 2100 m each year, gene flow between these and animals dispersing from the lowlands could be very substantial in some years. Such gene flow—depending on the timing of spring at both elevations—would be expected to inhibit if not prevent genetic differentiation along our altitudinal transect.

Numbers of this species are consistently too low for mark-recapture experiments to hold much promise as a test of the altitudinal-migration hypothesis. If genetic markers can be found to facilitate identification of low-elevation animals, they would be useful for documenting movements—but if gene flow is frequent, such markers are unlikely to be found. In the meantime, detailed seasonal data for a variety of localities are very desirable.

ACKNOWLEDGMENTS

This research forms part of the California Agricultural Experiment Station Project CA-D*-AZO-3994-H, "Climatic Range Limitation in Phytophagous Lepidopterans." I thank Leslie V. Smith for making his Sacramento data available for use in this paper.

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SEASONAL MICROHABITAT RELATIONSHIPS OF BLUE GROUSE IN SOUTHEASTERN IDAHO

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ABSTRACT.—Microhabitat characteristics of blue grouse (*Dendragapus obscurus*) were analyzed in breeding and wintering habitats in southeastern Idaho. Breeding habitats typically were open sagebrush (*Artemisia* spp.), mixed shrub, mountain mahogany (*Cercocarpus ledifolius*), and maple (*Acer grandidentatum*) stands on east to south facing aspects of slopes below 2100 m elevation. Breeding blue grouse selected areas with approximately a 50:50 or greater open to cover ratio. Blue grouse selected areas with higher tree coverage than available on average within the mixed shrub vegetation type. Hens with broods preferred sites with relatively tall (>50 cm) herbaceous vegetation. During autumn and winter, blue grouse preferred high elevation (>2285 m) stands of open (50% tree cover) conifer. Douglas-fir (*Pseudotsuga menziesii*) were preferred as winter roost trees. Sites selected in winter had significantly more Douglas-fir than those selected in autumn.

Blue grouse occur throughout western North America. Substantial work on this species has been conducted on Vancouver Island, British Columbia (e.g., Bendell and Elliott 1966, 1967, Fowle 1960, Zwickel and Bendell 1967, Lewis and Zwickel 1980). Blue grouse also have been studied throughout the Rocky Mountains (Marshall 1946, Caswell 1954, Heebner 1956, Blackford 1958, Boag 1966, Maestro 1971, Harju 1974, Weber 1975).

Most reports have concerned breeding behavior, with relatively little work being done on habitat requirements. Studies on blue grouse habitat typically have been qualitative in nature, relating grouse to general habitat categories (e.g., Marshall 1946, Caswell 1954, Heebner 1956, Bendell and Elliott 1966) or breeding habitat (Mussehl 1960, 1963, Maestro 1971, Martinka 1972, Weber 1975, Lewis 1981). Except for some analyses of male hooting sites (Martinka 1972, Lewis 1981), little quantitative information on blue grouse has been reported.

To adequately manage habitat for blue grouse, we must know their relationship to patterns of macro- and microhabitat characteristics. We previously described the macrohabitat relationships of blue grouse in southeastern Idaho (Stauffer and Peterson 1985). Here we address the microhabitat characteristics of blue grouse. Our objectives are to quantitatively describe habitats used by blue grouse for breeding and wintering and to compare characteristics of used habitats to available habitats.

Funding was provided by the USDA Forest Service. All personnel of the Montpelier Ranger District are gratefully acknowledged for their assistance throughout the fieldwork. B. S. Cade and B. A. Schrader were field assistants. Reviews of the manuscript by J. J. Spillett, E. O. Garton, M. Hironaka, E. G. Bizeau, R. K. Steinhorst, B. R. Noon, P. G. Stettenheim, and G. H. Cross are appreciated.

STUDY AREA AND METHODS

We examined blue grouse habitat relationships on the western portion (108,000 ha) of the Montpelier District of the Caribou National Forest, Bear River Range of the Wasatch Mountains in southeastern Idaho.

We classified the study area into eight relatively discrete vegetation types based on the dominant (according to density) tree and shrub species. Four open vegetation types (44% of the area) were most common at lower (<2130) elevations: sagebrush, mixed shrub, mountain mahogany, and bigtooth maple. Four forested vegetation types (56% of the area) were most common at mid and high

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elevation (>2130 m): aspen (*Populus tremuloides*), aspen/conifer mixed; dense conifer; and open conifer. We have described the floristic character of each vegetation type elsewhere (Stauffer and Peterson 1985).

We spent 1593 h (spring, 322 h; summer, 543 h; autumn, 296 h; winter, 432 h) searching for grouse from May 1979 through May 1981. Searching effort was distributed among the vegetation types in approximate proportion to their occurrence on the study area.

Each time a grouse (or group) was flushed, we used the location as the center of a 0.01 ha circular plot for which we recorded: percent of area within 40 m composed of coniferous or deciduous cover or open; canopy height and average height of herbaceous vegetation; number of woody stems <7 cm dbh in 2 perpendicular arm-width transects across the plot; number of trees by species within 6 dbh categories (7.0–15.0 cm, 15.1–23.0 cm, 23.1–38.0 cm, 38.1–53.0 cm, 53.1–69.0 cm, >69 cm dbh); and vegetation type.

We recorded 120 sets of plot data at random locations, 60 in the mixed shrub type and 60 in the maple vegetation type, to sample breeding habitat characteristics available to blue grouse.

We calculated means for data recorded in the 0.01 ha plots at grouse locations for various combinations of vegetation types and season to describe the characteristics of sites selected. For 38 winter roost trees, we measured a second set of plot data at the nearest potential roost tree that had no evidence of use. Additional data recorded at roost trees included tree species, diameter, and presence or absence of dwarf mistletoe (*Arceuthobium* spp.) infestation. We evaluated differences between used and unused sites with a paired *t*-test.

Prior to statistical analyses, all data were checked for normality, and those variables found to be nonnormal were transformed (log, square-root, or arc-sine) to achieve a more normal distribution.

RESULTS AND DISCUSSION

Blue grouse used a variety of vegetation types (Table 1). The open vegetation types (sagebrush, mixed shrub, mountain mahogany, and maple) were used primarily during spring and summer. These types constitute breeding habitat. The dense and open conifer types were used most heavily in fall and winter, although the open conifer type also was used in spring and summer. These use patterns are similar to those recorded elsewhere for the intermountain region (Marshall 1946, Caswell 1954, Heebner 1956, Mussehl 1960, 1963, Boag 1966, Zwickel et al. 1968, Maestro 1971, Harju 1974, Weber 1975).

In spring and summer, junipers (*Juniperus* spp.) and bigtooth maple were most commonly associated with blue grouse (32% and 52% of 227 observations, respectively). We found Douglas-fir and subalpine fir (*Abies lasiocarpa*) at 73% and 53% of 191 fall and winter observations, respectively. Additionally, limber pine (*Pinus flexilis*) was noted at 47% of 57 winter Blue Grouse observations (Stauffer 1983). Common shrubs at 227 blue grouse locations in spring and summer were sagebrush (72% occurrence), snowberry (*Symphoricarpos* spp., 54%), bitterbrush (*Purshia tridentata*, 27%). Snowberry (72%), sagebrush (57%), chokecherry (*Prunus virginiana*, 28%), and snowbrush (*Ceanothus velutinus*, 19%) most commonly occurred at 134 fall observations (Stauffer 1983).

CHARACTERISTICS OF BREEDING HABITAT

Sites used by blue grouse (Table 2) differed among the four open vegetation types, based on 10 microhabitat characteristics [Multivariate Analysis of Variance (MANOVA, $P<001$)]. Although habitat characteristics differed among the vegetation types, used sites were all relatively open, with the highest cover of about 60% conifer and deciduous cover occurring in the mountain mahogany vegetation type. Use of open areas by blue grouse during spring and summer has been documented throughout their range (Marshall 1946, Caswell 1954, Mussehl 1960, 1963, Boag 1966, Zwickel et al. 1968, Martinka 1972, Harju 1974, Weber 1975, and Lewis 1981).

We found no difference between spring and summer sites used by blue grouse in sagebrush (Hotelling's T^2, $P>0.05$). The data reflected the openness of this habitat (Table 2), but the presence of some trees indicated that areas with at least some taller cover were pre-

TABLE 1. Distribution of blue grouse plot observations among the vegetation types studied; southeastern Idaho, 1979–1981.

	Percent of observations					
Vegetation type	Brood	Hooting	Spring	Summer	Autumn	Winter
Sagebrush	12	7	25	14	2	0
Mixed shrub	9	25	17	14	6	0
Mountain mahogany	0	21	7	9	11	0
Maple	36	45	34	35	2	0
Aspen	9	0	0	3	4	0
Aspen/conifer	3	0	4	1	8	0
Dense conifer	3	0	0	3	14	18
Open conifer	27	2	13	23	54	82
Number of observations	33	44	71	80	134	56

Spring and summer data exclude brood and hooting observations.

TABLE 2. Means of habitat characteristics recorded for 0.01 ha circular plots at blue grouse locations and random locations in open habitats in southeastern Idaho, 1979–1981.

	Sagebrush	Mountain mahogany	Mixed shrub		Maple	
Variable	$n = 33$	$n = 36$	Spring-autumn $n = 45$	Random obs. $n = 60$	Spring-summer $n = 84$	Random obs. $n = 60$
Coniferous cover (%)	2.6(0.6)[a]	4.0(1.1)	3.1(0.9)	* 0.2(0.1)	5.0(0.6)	5.8(0.8)
Deciduous cover (%)	8.4(1.7)	56.0(2.5)	26.4(2.8)	*15.4(2.0)	43.6(1.9)	49.4(3.1)
Open (%)	88.8(1.8)	40.0(2.4)	70.5(2.7)	*84.0(2.0)	51.4(1.8)	44.8(3.1)
Tree canopy cover (%)	8.2(3.3)	36.9(4.7)	8.3(2.4)	* 4.1(1.4)	23.8(2.5)	24.6(4.0)
Ground cover (%)	48.0(4.4)	42.6(3.9)	49.0(3.2)	*57.2(2.1)	56.5(2.5)	*78.6(2.1)
Canopy height (m)	1.3(0.2)	3.4(0.1)	2.0(0.2)	* 1.5(0.1)	3.5(0.2)	3.6(0.3)
Stems <7 cm dbh/ha	847(372)	2428(406)	7400(1590)	*4056(460)	4395(435)	4092(462)
Trees/ha	15(8)	352(50)	49(19)	40(19)	249(36)	305(60)
Coniferous trees/ha	12(6)	22(10)	2(2)	0	27(9)	18(7)
Deciduous trees/ha	3(3)	330(49)	47(19)	40(19)	222(35)	287(60)

[a] Standard error.

*Indicates a significant ($p<0.05$) difference based upon a t-test between the grouse observations and random observations in the vegetation type.

ferred. Mussehl (1963) and Weber (1975) noted that blue grouse often were found near clumps of trees in sagebrush stands.

Mountain mahogany was used spring through autumn and had the highest tree cover of the four open vegetation types (Table 2). Percent ground cover was the only characteristic that differed among spring, summer, and autumn observations and was highest in summer and autumn (47.8% and 56.0%, respectively) and lowest in spring (22.1%). Twenty-one percent of the hooting observations were in mountain mahogany, but no broods were found here.

Sites selected by blue grouse in the mixed shrub vegetation type did not differ among spring, summer, and autumn observations (MANOVA, $P>0.05$). However, microhabitat characteristics of sites used were different from a random sample of 60 sites in this type (Hotelling's T^2, $P<0.001$, Table 2). Percent coniferous and deciduous cover, percent tree canopy cover, and density of small stems were higher and percent open area and ground cover were lower at sites used by grouse than at random sites. Thus, blue grouse are selecting areas within the mixed shrub vegetation type with higher than average woody cover (see also Weber 1975).

We found differences in sites used between spring and summer by blue grouse in the maple vegetation type (Hotelling's T^2, $P < 0.01$). Percent coniferous cover and density of coniferous trees were higher and percent deciduous cover was lower at sites used in spring (spring $\bar{x} = 7.1\%$, 59/ha, and 37.6%, respectively; summer $\bar{x} = 3.4\%$, 2/ha, and 48.3%, respectively; df = 79 and $t = 3.2$, 4.1, and 2.3, respectively.) During spring, grouse often were associated with junipers in the maple type, which may provide cover prior to leafout of the deciduous trees. Weber (1975) found that male blue grouse often were associated with junipers on breeding areas in Utah. Except for percent ground cover, which was lower at used sites, ($t = 6.1$, $P<0.01$), habitat characteristics were not different between random sites and those used in maple vegetation types (Table 2). Thus, blue grouse were not selecting for any particular characteristic of the maple vegetation type.

These open types provide suitable habitat for hooting by male blue grouse. Lewis (1981) reported tree cover of 6.6% and canopy height of 3.3 m at hooting sites on Vancouver Island. In Montana, Martinka (1972) found a tree crown cover of 30% at male display sites and Maestro (1971) noted that breeding blue grouse preferred areas of 41%–50% tree cover in Utah. These values are comparable to the characteristics of habitats where we found blue grouse breeding in southeastern Idaho (Table 2). The primary characteristic of hooting habitat is an interspersion of open areas with taller woody cover (Weber 1975).

Blue grouse broods selected areas with relatively high herbaceous cover. Within the maple vegetation type, mean height of herbaceous vegetation at 12 brood locations was 50.8 cm (SE = 4.0), which was higher than that of 35 other summer observations in maple ($\bar{x} = 38.0$ cm, SE = 3.4, $t = 2.16$, df = 45). In the open conifer vegetation type, mean herbaceous vegetation height at nine brood locations was 63.3 cm (SE = 14.8), whereas that for 19 other summer observations in open conifer was 31.0 cm (SE = 5.0, $t = 2.61$, df = 26). Sample sizes of broods in sagebrush (n = 4) and mixed shrub (n = 3) were not adequate for testing. Mussehl (1963) felt that herbaceous cover at least 50 cm tall, interspersed with bare ground to provide travel lanes, was the most important aspect of good blue grouse brood cover. Additionally, clumps of small trees and shrubs may enhance brood habitat by providing nesting sites and protection from predators (Mussehl 1960, 1963, Weber 1975) and may be particularly important in late summer when herbaceous cover becomes dessicated or is heavily grazed (Zwickel 1973).

These results indicate that a variety of vegetation types can be managed as blue grouse breeding habitat. No major differences between seasons within each type implies that maintaining habitat characteristics for each type within the levels reported in Table 2 should provide adequate conditions for breeding and brood rearing. Except for tall herbaceous cover for broods, different characteristics need not be provided for different stages of the breeding season. Although we did find some blue grouse breeding at high elevation, these areas probably are not as important for breeding as low elevation open habitats (Stauffer and Peterson 1985).

CHARACTERISTICS OF CONIFEROUS HABITATS

Blue grouse selected sites in dense conifer stands during fall and winter with about 65%–69% coniferous tree cover (Table 3). Since mean percent tree canopy cover at blue grouse locations in autumn was 45%, blue grouse selected the more open areas within dense conifer. Although tree density in dense conifer was similar at autumn and winter locations, significantly ($t = 2.15$, df = 27) more Douglas-fir were found at winter locations of blue grouse.

Blue grouse selected open conifer stands that had approximately a 50:50 conifer cover to open ratio. Caswell (1954) found that blue grouse selected open conifer slopes in winter with islands of subalpine and Douglas-fir. Percent tree canopy cover was relatively low in all seasons, averaging 32%–44% (Table 3).

Density of small stems at blue grouse locations in open conifer was lower for all seasons compared to those of other vegetation types (Tables 2 and 3). Densities of subalpine fir at grouse locations did not vary significantly among seasons, but Douglas-fir densities were higher ($t = 5.84$, df = 115) at winter locations than those for autumn (Table 3). In winter, this species is used for food and as roost sites (Marshall 1946).

Winter Roost Trees

We compared trees used as winter roosts and for feeding with those not used. Of 38 roost trees, 36 (95%) were Douglas-fir and one each (2.5%) were subalpine fir and Engelmann spruce (*Picea engelmannii*). Of 343 conifers recorded along randomly located transects in three wintering areas, 57% were Douglas-fir, 33% were subalpine fir, 5% were limber pine, 2% were Engelmann spruce, and 3% were lodgepole pine (*Pinus contorta*) Thus, Douglas-fir were preferred as roost trees.

TABLE 3. Mean vegetation characteristics recorded for 0.01 ha circular plots at blue grouse locations in the dense and open conifer vegetation types in southeastern Idaho, 1979–1981.

	Dense conifer		Open conifer			
Variable	Fall $n = 19$	Winter $n = 10$	Spring $n = 9$	Summer $n = 28$	Autumn $n = 71$	Winter $n = 46$
Coniferous cover (%)	68.7(2.7)[a]	65.5(2.7)	45.0(2.9)	48.9(2.2)	47.7(1.8)	44.2(1.8)
Deciduous cover (%)	1.8(0.8)	1.7(1.0)	1.1(1.1)	3.0(1.3)	2.5(0.5)	4.8(1.3)
Open (%)	28.9(2.8)	33.6(3.1)	53.9(2.3)	48.0(2.1)	49.7(1.8)	50.9(2.0)
Tree canopy cover (%)	45.1(7.1)	—	33.7(9.6)(n=3)[b]	38.5(6.3)	31.6(4.1)(n=65)	40.5(8.5)(n=11)
Ground cover (%)	28.4(5.2)	—	14.4(8.3)	41.8(3.8)	32.4(2.5)	5.8(2.2)
Canopy height (m)	19.8(2.2)	22.8(1.2)	15.7(2.0)	13.8(1.4)	14.6(0.9)	18.8(1.1)
Stems < 7 cm dbh/ha	1026(247)	391(157)	134(71)	495(163)	1275(332)	291(77)
Trees/ha	426(126)	350(72)	256(67)	275(40)	294(40)	361(68)
Deciduous trees/ha	16(11)	0	0	18(9)	17(6)	15(10)
Subalpine fir/ha	195(72)	60(34)	33(33)	61(21)	140(33)	143(54)
Douglas-fir/ha	63(25)	180(57)	189(65)	154(38)	110(25)	193(30)
Lodgepole pine/ha	63(41)	50(40)	0	11(11)	7(4)	0

[a] Standard error.

[b] Where noted, sample size is smaller because the variable was not recorded for roost tree observations.

TABLE 4. Mean vegetation characteristics at 38 roost tree sites used by blue grouse and nearby unused sites; southeastern Idaho, 1979–1981.

Variable	Mean (SE)		Significance[a]
	Used	Not used	
Coniferous cover (%)	50.3(1.9)	44.5(2.1)	$p < 0.01$
Open (%)	45.2(1.9)	50.2(1.9)	$p < 0.01$
Canopy height (m)	21.5(0.9)	20.5(1.0)	$p > 0.20$
Trees/ha	321(32)	303(34)	$p > 0.20$
Trees 7–15 cm dbh/ha	100(24)	129(27)	$p > 0.20$
Trees 15–33 cm dbh/ha	97(23)	87(16)	$p > 0.20$
Trees > 33 cm dbh/ha	124(13)	87(10)	$p < 0.02$
Subalpine fir/ha	68(21)	87(26)	$p > 0.20$
Douglas-fir/ha	218(25)	179(22)	$p > 0.20$
Limber pine/ha	24(10)	24(10)	$p > 0.20$
Roost tree dbh (cm)	49.2(3.1)	42.8(2.4)	$p < 0.05$

[a] Represents the significance of a paired t-test for differences between used and unused trees for the variable.

A paired *t*-test revealed significant differences for four variables measured at used and unused trees (Table 4.) Coniferous cover was greater and percent of area open was less at used trees. Used trees had a larger dbh and the density of large (> 33 cm dbh) trees was higher at used trees, as measured within circular plots (Table 4). Thus, within open conifer stands, blue grouse were selecting trees for roosting and feeding that were in denser clumps and were larger than trees not used. Roost trees often were in clumps rather than solitary. Although not investigated here, nutritional differences in the needles of different trees might influence roost and feeding tree selection, as has been found for spruce grouse (*Dendragapus canadensis*, Ellison 1976).

Blue grouse appeared to prefer large Douglas-fir that had dense foliage. The dense foliage may provide protection from predators and weather, which often is harsh at high elevations in winter.

Maintenance of open, high elevation stands of conifers, especially those containing Douglas-fir, should provide adequate winter habitat for blue grouse. Such stands have low commercial value; thus winter habitat of blue grouse probably is not threatened in southeastern Idaho.

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FALL DIET OF BLUE GROUSE IN OREGON[1]

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ABSTRACT.—The early fall diet of Oregon blue grouse (*Dendragapus obscurus pallidus*) from Wallowa County, Oregon, was determined from 145 crops obtained during 1981 and 1982. Of more than 50 plant and animal foods in the diet, short-horned grasshoppers (*Acrididae*), prickly lettuce (*Lactuca serriola*), yellow salsify (*Tragopogon dubius*), wild buckwheat (*Eriogonum* spp.), and snowberry (*Symphoricarpos albus*) occurred in 30% or more of the crops and collectively amounted to 68% of the diet by weight. Seven of the 12 most common foods were consumed differentially by the four sex and age classes of birds. Results indicated that blue grouse foraged in forest and grassland habitats.

In 1981, a study was established to determine the early fall diet of the Oregon blue grouse in Wallowa County, Oregon. Our objectives were to compare the diet of grouse in this area with diets from other locations, especially within the range of this subspecies, and to determine if dietary differences existed among the sex and age classes.

Previous work indicated that western larch (*Larix occidentalis*) needles were one of the most important foods from August through October for blue grouse in northcentral Washington and Idaho (Beer 1943, Boag 1963). Fir (*Abies* spp.) and Douglas-fir (*Pseudotsuga menziesii*) needles, staple winter foods, also composed a major portion of the fall diet (Beer 1943, Stewart 1944, Marshall 1946, Boag 1963). Bearberries (*Arctostaphylos uva-ursi*) likewise were noted as common foods by Beer (1943) and Boag (1963). Grasshoppers and ants composed most of the animal foods in the fall diet of blue grouse (Beer 1943, Stewart 1944, Marshall 1946, Martin et al. 1951, Boag 1963, King and Bendell 1982).

Few differences in the diets of adult and immature blue grouse during late summer and fall have been noted. King and Bendell (1982) commented that from late July through September adults and juvenile blue grouse (*D. o. fuliginosus*) on Vancouver Island consumed approximately the same types and amounts of foods. Beer (1943), in Idaho, reported that adults consumed more larch needles than did immatures during August, but by September the diets were similar.

A contrasting work by Boag (1963) revealed that greater amounts of larch needles were eaten by adults than by immatures during September and October, but no other differences in the consumption of the major foods by the sex and age classes of blue grouse were found.

STUDY AREA AND METHODS

In Wallowa County blue grouse typically inhabit bunchgrass ridges, which are dissected by draws that are timbered on the north-facing aspect. Elevation ranges from 600 to 1500 m. Bunchgrass communities are dominated by bluebunch wheatgrass (*Agropyron spicatum*) and Idaho fescue (*Festuca idahoensis*). Dominant forbs are wild buckwheat (*Eriogonum* spp.) and arrow-leaf balsamroot (*Balsamorhiza sagittata*). Timbered draws are dominated by ponderosa pine (*Pinus ponderosa*), Douglas-fir, true firs, and western larch. Shrub understories are composed of mallow ninebark (*Physocarpus malvaceus*), snowberry (*Symphoricarpos albus*), big huckleberry (*Vaccinium membranaceum*), creambush ocean-spray (*Holodiscus discolor*), currants (*Ribes* spp.), and shiny-leaf spiraea (*Spiraea betulifolia*). Idaho fescue and pinegrass (*Calamagrostis rubescens*) are the most common grasses in the understories. Grazing by domestic livestock occurs on most

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TABLE 1. Fall diet of blue grouse, Wallowa County, Oregon, 1981–1982.

Food item	Parts consumed	Frequency (%) (n = 145)	Weight (%) (n = 83)[a]
PLANTS			
Prickly lettuce (*Lactuca serriola*)	seed heads	43	17
Yellow salsify (*Tragopogon dubius*)	seed heads	41	9
Wild buckwheat (*Eriogonum* spp.)	leaves	33	5
Snowberry (*Symphoricarpos albus*)	berries	30	5
Douglas-fir (*Pseudotsuga menziesii*)	needles, buds	16	2
Elkhorns clarkia (*Clarkia pulchella*)	seed heads	16	tr[b]
Unidentified Gramineae	leaves, seeds	12	tr
Western larch (*Larix occidentalis*)	needles	10	4
Clover (*Trifolium* spp.)	leaves	10	1
Everlasting (*Antennaria* spp.)	leaves	7	1
Serviceberry (*Amelanchier alnifolia*)	berries	6	1
Ponderosa pine (*Pinus ponderosa*)	seeds	6	tr
Dwarf mistletoe (*Arceuthobium* spp.)	entire plant	5	4
Smartweed (*Polygonum* spp.)	seeds	5	tr
Unidentified Compositae	seed heads	5	tr
Lodgepole pine (*Pinus contorta*)	seeds, needles	4	tr
Filaree (*Erodium circutorium*)	seeds, leaves	4	tr
Selaginella (*Selaginella* spp.)	entire plant	3	tr
Hawthorne (*Crataegus douglasii*)	berries, stems	3	7
Elderberry (*Sambucus cerulea*)	berries	3	3
Currant (*Ribes* spp.)	berries	3	2
Huckleberry (*Vaccinium membranaceum*)	berries	3	1
Unidentified Ericaceae	berries	1	1
Juniper (*Juniperus occidentalis*)	berries	1	tr
Yew (*Taxus brevifolia*)	needles	1	tr
Engelmann spruce (*Picea engelmannii*)	needles	1	tr
Fir (*Abies* spp.)	needles	1	tr
Microseris (*Microseris* spp.)	seed heads	1	tr
Dandelion (*Taraxacum* spp.)	seed heads	1	tr
Sorrel (*Rumex* spp.)	leaves	1	tr
Bedstraw (*Galium* spp.)	leaves, seeds	1	tr
Strawberry (*Fragaria virginiana*)	berries	1	tr
Unidentified Leguminosae	seeds	1	tr
Brome (*Bromus* spp.)	leaves	1	tr
Bentgrass (*Agrostis* spp.)	stems	1	tr
Unidentified plant material	leaves	4	tr
ANIMALS			
Short-horned grasshoppers, Acrididae		46	32
Ants, Formicidae		24	1
Long-horned grasshoppers, Tettigoniidae		20	3
Spittle bugs, Cercopidae		7	tr
Ground beetles, Carabidae		5	tr
Ladybird beetles, Coccinellidae		4	tr
Stink bugs, Pentatomidae		3	tr
Darkling beetles, Tenebrionidae		3	tr
Unidentified Insecta larvae		3	tr
Unidentified Insecta		2	tr
Chinch bugs, Lygaeidae		1	tr
Stink bugs, Scutelleridae		1	tr
Flies, Diptera		1	tr
Spiders, Araneida		1	tr
Sawflies, Tenthredinidae		1	tr
Yellow jackets, Vespidae		1	tr
Treehoppers, Membracidae		1	tr
Plant bugs, Miridae		1	tr
Stilt bugs, Berytidae		1	tr
Unidentified Hemiptera		1	tr

[a] Weight was obtained only for crops obtained during 1981.

[b] All items marked "tr" combined amounted to 1% of the diet by weight.

sites. Many of the forest stands are managed for commercial timber production and some have extensive road systems.

From 28 August through 29 September of 1981 and 1982, 145 crops containing food (39 adult males, 34 adult females, 39 immature males, and 33 immature females) were obtained from hunter-killed blue grouse. The majority of crops (61%) were from birds taken between 28 August and 3 September, 33% came from the second week, and the remainder from birds killed from 11 to 29 September. The four sex age classes were represented similarly through time; for example 59% of the crops from immature males and females and 63% from adult males and females were collected during the first week. Ages of immatures in weeks was determined by stage of molt sequence of primary feathers (Zwickel and Lance 1966) and ranged from 9 to 17 weeks ($\bar{x} = 13$ weeks) (Redfield and Zwickel 1976). Contents of the crops were dried in an oven at 50 C for three days, identified and weighed. Contents of the 62 crops collected in 1982 were inadvertently destroyed before weighing. A subjective evaluation of the relative amounts of foods in the 1982 sample revealed that they were essentially identical to the 1981 sample. Frequencies of occurrence of the most common foods were tested among the four sex and age classes with Chi-square analysis (Snedecor and Cochran 1967:20). Analysis of variance (Snedecor and Cochran 1967:258) was used to test for differences in weights of foods eaten by the sex and age classes.

RESULTS AND DISCUSSION

More than 50 plant and animal foods were consumed by blue grouse (Table 1). Of these, short-horned grasshoppers, prickly lettuce, yellow salsify, wild buckwheat, and snowberry were consumed at a frequency of 30% or more; collectively, these foods accounted for 68% of the diet by weight. Five additional plant foods and two groups of insects were found in 10% to 29% of crops and contributed 11% of the diet by weight. Of the 12 most common foods, 7 were consumed differentially by the sex or age classes of blue grouse (Table 2).

Short-horned grasshoppers (*Acrididae*), an important summer food of blue grouse (Stewart 1944, Marshall 1946, Martin et al. 1951), were found in 46% of the crops and contributed 32% by weight. The frequency of short-horned grasshoppers in the diet was higher ($P < 0.001$) for immatures (64%) than for adults (27%). Prickly lettuce was the second most frequent item in the fall diet and was consumed with similar frequency by all sex and age groups. Females, of both ages, consumed yellow salsify ($P \sim 0.02$) and wild buckwheat ($P \sim 0.06$) more commonly than did males. Previous work (Boag 1963) indicated that prickly lettuce, yellow salsify, and wild buckwheat were only minor components of the fall diet.

Snowberries were consumed equally by all sex and age classes and apparently are a more important fall food in Oregon than elsewhere within the range of the Oregon blue grouse (Beer 1943, Stewart 1944, Boag 1963). No differential use by the sex and age classes of blue grouse were found for ants, Douglas-fir needles, or unidentified grasses. Both ants and Douglas-fir needles were reported as common in the fall diet of blue grouse (Stewart 1944, Boag 1963).

Clarkia (*Clarkia pulchella*) and clover (*Trifolium* spp.) were more frequently ($P \sim 0.06$) consumed by adults than by immatures. Clarkia was more common in the diet of blue grouse from Oregon (9% to 24% frequency) than from Washington (1% to 3% frequency) (Boag 1963), whereas the use of clover was similar. Clarkia was considered a food rejected by blue grouse on Vancouver Island (King and Bendell 1982). Long-horned grasshoppers (Tettigoniidae) were consumed more frequently ($P \sim 0.05$) by immatures than by adults.

Needles of western larch were the most important food in the diet of blue grouse during September and October in eastern Washington, where they were consumed with a frequency of 28% to 60% (Boag 1963). Beer (1943) found that larch needles composed 46.9% of the diet by volume during August, but they dropped to 2.3% in September. In our study, larch needles were consumed in a moderate amount (10% frequency, 4% weight), but were used most commonly by adult males ($P < 0.001$). Larch needles occurred in 28% of the crops from adult males and in only 3% to 6% of the other three groups. Boag (1963) found that adults utilized larch significantly more than did immatures, but he found no differences in use between adult males and adult females.

TABLE 2. Frequency of the 12 most common foods by sex and age classes of blue grouse, Wallowa County, Oregon, 1981–1982.

	Frequency (%)			
Food item	Adult male (n = 39)	Adult female (n = 34)	Immature male (n = 39)	Immature female (n = 33)
Prickly lettuce[a]	43	38	45	47
Yellow salsify[b]	35	50	28	53
Wild buckwheat[c]	25	35	28	47
Snowberry[a]	35	24	28	35
Clarkia[d]	20	18	5	12
Doulas fir[a]	18	9	20	15
Unidentified Gramineae[a]	15	9	13	9
Western larch[e]	28	6	3	3
Clover[d]	15	15	5	6
Short-horned grasshoppers[f]	18	38	63	65
Ants[a]	25	18	35	18
Long-horned grasshoppers[g]	10	15	28	24

[a] No significant differences among sex and age classes.

[b] Females > males, $P \sim 0.02$.

[c] Females > males, $P \sim 0.06$.

[d] Adults > immatures, $P \sim 0.06$.

[e] Adults males > all other, $P < 0.001$.

[f] Immatures > adults, $P < 0.001$.

[g] Immatures > adults, $P \sim 0.05$.

The average number of food items in a crop was 4.2. Average numbers of items ranged from 3.7 (adult females) to 4.6 (immature females), but no difference ($P > 0.25$) existed in the number of items/crop among the sex and age groups.

Our work revealed, in contrast to results of studies by Beer (1943), Stewart (1944), and Boag (1963), that most of the common early fall foods were consumed differentially by the sex and age groups of blue grouse. Greater consumption of short-horned and long-horned grasshoppers likely reflected availability of these groups during late August and September in Oregon and probably represented a retention of the feeding patterns of immatures from summer. Stewart (1944) reported a fivefold greater consumption of animal matter by immatures during summer. Likewise, the greater use of Elkhorns clarkia and clover by adults possibly represented a continuation of summer feeding habits. Beer (1943) found that adults ate more fruits, seeds, and green leafy material during summer than did immatures. By contrast, King and Bendell (1982) noted that the consumption of fruits, leaves, and flowers during late summer and early fall was similar between adult and immatures.

Of the four foods with the greatest frequency of use, yellow salsify and wild buckwheat were taken more commonly by females than males. The preponderance of prickly lettuce and yellow salsify seed heads and wild buckwheat leaves in the fall diet of blue grouse in Oregon was likely related to availability.

Adult males during August and September are solitary and commonly at higher elevations than adult hens and immatures (Marshall 1946, Boag 1963). In addition, our observations of habitat use by adult males during September indicated that they commonly are found in larch thickets, which may account for the greater use of larch needles by adult males.

The results of previous work (Beer 1943, Boag 1963) indicated that Oregon blue grouse foraged primarily in forested habitats during early fall, e.g., areas containing larch, Douglas-fir, true firs, and bearberry. In contrast, birds in this study made use of a broad range of foods and, presumably, foraging habitats. The two most important plant foods, prickly lettuce and yellow salsify, are introduced "weed" species. Both are common in bunchgrass communities, especially where the soil has been disturbed by the burrowing activities of smal mammals or by grazing and trampling by wild and domestic ungulates. Clarkia is common in disturbed areas (W. C. Krueger, persona communication). Wild buckwheat character istically is found in dry, open habitats (W. C. Krueger, personal communication). In addition, the importance of forested areas for foraging by blue grouse in Oregon is exemplified by the use of snowberry, western larch, and Douglas-fir.

ACKNOWLEDGMENTS

We wish to thank R. G. Anthony and R. L. Jarvis for their reviews of this manuscript.

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STATUS AND DISTRIBUTION OF CALIFORNIA GULL NESTING COLONIES IN WYOMING

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ABSTRACT.—Historically, two California Gull nesting colonies existed in Wyoming. In 1984 there were six breeding locations consisting of 10 different colonies that included approximately 7,273 nests. The increase in the California Gull nesting population in the state is probably a consequence of man-caused environmental changes that have resulted in the creation of additional breeding habitat and new food sources.

Breeding populations of California Gulls (*Larus californicus*) have increased in Washington State and throughout much of the western United States since the 1920s (Conover et al. 1979, Conover 1983). Reasons for the proliferation of this species include the construction of large water impoundments with isolated islands for nesting, as well as the gulls' exploitation of new man-made terrestrial food sources such as garbage dumps, other human refuse, and agricultural land (Conover 1983). Also, the California Gull has probably benefited from reduced human predation by egg and plumage hunters.

In this paper I present information on the distribution, population status, and habitat of recent California Gull nesting colonies in Wyoming. I also provide details on the history of each colony and give reasons for the population increase of this species in the state. My purpose is to provide baseline data on each colony and to clarify the literature on the current number of California Gull nesting colonies in Wyoming.

METHODS

In 1983 and 1984 I conducted a survey for California Gull breeding locations to obtain recent information on the distribution of nesting colonies in Wyoming. Between 4 April and 31 May 1984 seven aerial searches in fixed-wing aircraft were made for nesting areas of all colonial water birds, including California Gulls. Reservoirs, lakes, marshes or other potential breeding sites not observed during aerial flights were surveyed from the ground with binoculars or a spotting scope. Estimates of active nests were based on total ground counts except for one colony, where the number of nests was determined by a belt transect technique. All colonies were censused in 1984 except for the Molly Islands colony, Yellowstone Lake, Yellowstone National Park; and Bamforth Lake colonies, Albany County. Colonies were censused when most birds were in the late incubation or early hatching stages and based on one visit to each colony. A colony was defined as a geographically continuous group of breeding birds whose territorial boundaries are contiguous (Penney 1968). One exception was the Sand Mesa Wildlife Habitat Management Unit (WHMU), where several small breeding aggregations of California Gulls on man-made islands were treated as one colony.

Historical sources of information on California Gull nesting areas included a literature review, an examination of the files of the Wyoming Game and Fish Department, and contact with biologists, naturalists, bird-watchers, and others considered knowledgeable of California Gull breeding locations in the state.

COLONY DESCRIPTIONS AND HISTORIES

Bamforth Lake

McCreary (1939) considered the California Gull a common summer resident in Albany County and indicated that a small colony had existed since 1934 on an island in Bamforth Lake, 15 km northwest of Laramie (Fig. 1). In 1937 this nesting colony was about one-fourth as large as the Molly Islands, Yellowstone

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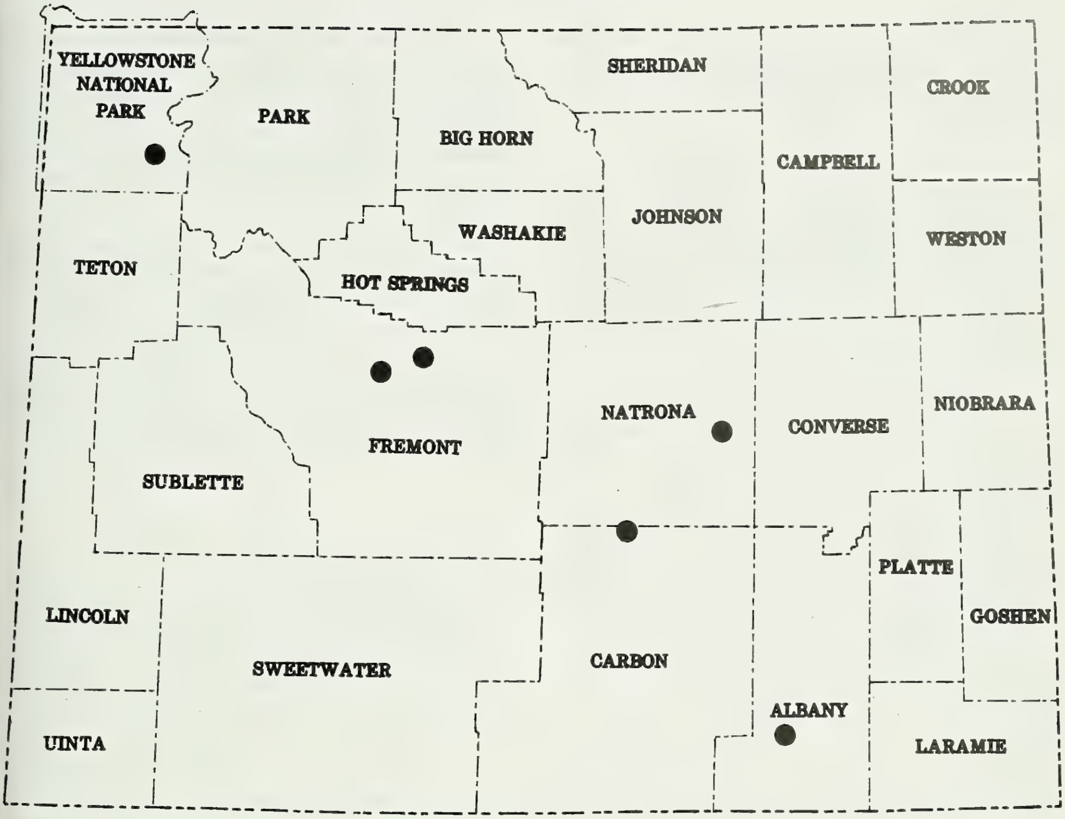

Fig. 1. Locations of California Gull nesting colonies in Wyoming, 1984.

Lake, colony in 1932 (McCreary 1939). Total numbers of California Gull nests in the Bamforth Lake colony ranged from a low of 1,364 in 1967 to 2,003 in 1968, with a mean of 1,842 between 1967 and 1972 (Kennedy 1973). In 1974 this colony contained 2,069 nests and increased to 2,470 nests in 1975 (Raper 1975). Approximately 5,000 gulls were estimated to be breeding at the Bamforth Lake colony in 1979 and 1980 (Pugesek 1983). In 1984 from 6,000 to 7,000 California Gulls appeared to be nesting at Bamforth Lake. In addition to breeding on Bamforth Island, the traditional nesting site, a portion of the California Gulls bred on a 0.4-ha natural island, about 0.5 km southwest of the main colony. Establishment of the new nesting colony in 1984 was probably in response to reduced nesting habitat. On 14 July 1983 Bamforth Island was 1.2 ha, which was 45% smaller than it was in 1975 (Raper 1975). The nesting island continued to decline in size throughout 1984 because of rising water levels caused by above normal precipitation and increased irrigation runoff. By 1 August Bamforth Island was completely inundated except for the tops of black greasewoods (*Sarcobatus vermiculatus*).

Bamforth Island is primarily composed of bare ground interspersed with dense patches of black greasewood. The new nesting island, Peninsula Island, had more vegetative cover because the colony was recently established. Predominant plants included black greasewood and prickly-pear cactus (*Opuntia* sp.) interspersed with grasses and forbs. Nesting associates at Bamforth Lake in 1984 included the Double-crested Cormorant (*Phalacrocorax auritus*, 72 active nests), Snowy Egret (*Egretta thula*, 7 active nests), Black-crowned Night-Heron (*Nycticorax nycticorax*, 1 active nest), and Herring Gull (*Larus argentatus*, 3 active nests).

Bamforth Lake is a naturally occurring lake, almost entirely in private ownership, except for small portions under jurisdiction of the U.S. Fish and Wildlife Service and set aside as

Bamforth National Wildlife Refuge. Because access is restricted, Bamforth Lake receives minimal use from the public.

Pathfinder Reservoir

The nesting colony at Pathfinder Reservoir, an irrigation impoundment on the North Platte River, is about 70 km northeast of Rawlins, Carbon County (Fig. 1). Although California Gulls were first reported to be breeding here on 7 May 1982 by T. Varcelli, it is unknown when the colony was initiated. On 15 June 1984, I counted 683 California Gull nests. Birds were nesting on a 5.2-ha island, hereafter called Bird Island, about 0.8 km from the mainland and near the mouth of Sand Creek. The island is well vegetated, with silver sagebrush (*Artemisia cana*), gray rabbitbrush (*Chrysothamnus nauseosus*), sand dock (*Rumex venosus*), plains cottonwood (*Populus sargentii*), and willow (*Salix* sp.) being most common. Other colonial waterbirds on Bird Island were the American White Pelican (*Pelecanus erythrorhynchos*, 245 active nests), Double-crested Cormorant, 126 active nests; Great Blue Heron (*Ardea herodias*, 38 active nests), and Caspian Tern (*Sterna caspia*, 15 to 20 active nests).

Although portions of Pathfinder Reservoir receive considerable recreational use, presently human disturbance in the vicinity of Bird Island appears minimal.

Ocean Lake WHMU

Ocean Lake, about 24 km northwest of Riverton, Fremont County (Fig. 1), is a manmade lake that was formed in 1926 from irrigation return flow and seepage from Pilot Butte Reservoir (Serdiuk 1965). California Gulls started breeding here in small numbers during the early 1950s (W. Higby, personal communication). R. Klataske (1970) counted 550 nests on Third Point Island and 110 nesting pairs on Gull Island, and he estimated that about 2,000 California Gulls nested at Ocean Lake in 1970. The one colony that I discovered at Ocean Lake in 1981 was deliberately destroyed by humans. There were 609 California Gull nests at Ocean Lake on 14 May 1983. All gulls were breeding on Peninsula Island in the southeastern portion of the lake. This nesting colony increased to 775 nests on 19 May 1984.

The 0.4-ha nesting island was almost void of vegetation except for sparse black greasewood on its southern portion and cattails (*Typha latifolia*) along the southwestern and eastern shorelines. The only nesting associate in 1984 was the Double-crested Cormorant (205 active nests).

Ocean Lake is included in Ocean Lake WHMU and managed by the Wyoming Game and Fish Department. It is heavily used for recreation during the nesting season. Except as noted in 1981, human disturbance of breeding California Gulls has not been a serious problem because shallow water in the vicinity of the nesting island discourages boating activity.

Sand Mesa WHMU

Sand Mesa WHMU, managed by the Wyoming Game and Fish Department, is approximately 32 km northeast of Riverton, Fremont County (Fig. 1). It consists of several small reservoirs designed primarily for waterfowl production. I counted 181 California Gull nests at Pond No. 1 on 15 May 1983. This was the first year that gulls bred here (K. Asay, personal communication). California Gulls were nesting on six manmade islands that averaged about 0.013 ha. Islands were composed of cobble and were generally void of vegetation. The nesting colony contained 162 nests on 12 May 1984, which is 19 fewer nests than in 1983. This decline was most likely caused by the addition of more cobble, making islands dome shaped and less suitable as nesting substrate. Nesting associates in 1984 included the Double-crested Cormorant (21 active nests) and Snowy Egret (from 1 to 2 active nests). When I rechecked the colony 22 June 1984, all California Gull nests had been destroyed, most likely from human intervention.

Soda Lake

Soda Lake, located 3 km north of Casper, Natrona County (Fig. 1) occurs naturally. However, the lake has increased in size because waste water is added to it by the Amoco Oil Refinery. California Gulls have nested here since the late 1950s (O. K. Scott, personal communication). In 1970 G. Dern estimated that approximately 400 breeding gulls were present. There were four California Gull nesting colonies at Soda Lake when I surveyed it in 1984.

MANMADE ISLAND.—This 1.3-ha island on the southeast portion of Soda Lake was developed after the 1983 nesting season. Thus, 1984 was the first year that California Gulls bred here. On 22 May 1984, I estimated that 1,907 ± 204 (SE) active California Gull nests were present. Nesting associates included the Double-crested Cormorant (58 active nests), Snowy Egret (1 active nest), and Ring-billed Gull (*Larus delawarensis*, 70 active nests). There was dense vegetative cover on this island. Predominant species were silver sagebrush and cheat grass (*Bromus tectorum*). Other common plants included green rabbitbrush (*Chrysothamnus viscidiflorus*), prickly-pear cactus (*Opuntia polyacantha*), and other grasses.

RATTLESNAKE ISLAND.—This 0.2-ha natural island near the east end of Soda Lake was first utilized for nesting by California Gulls in 1984. On 21 May 1984 I counted 560 active gull nests. One pair of Caspian Terns also bred here. Rattlesnake Island was covered with grasses interspersed with black greasewood and prickly-pear cactus when censused for gulls.

EAST ISLAND.—On 22 May 1984 I found 24 active California Gull nests on this 0.08-ha natural island. Nesting associates included the Double-crested Cormorant (10 active nests) and Black-crowned Night-Heron (1 active nest). This island is disappearing because of high water levels at Soda Lake. It is void of vegetation except for sparse cheat grass, other grasses, black greasewood, and prickly-pear cactus.

WEST ISLAND.—I counted 93 active California Gull nests on this 0.12-ha natural island 22 May 1984. Other colonial waterbirds nesting here were the Double-crested Cormorant (290 active nests), Snowy Egret (2 active nests), and Black-crowned Night-Heron (2 active nests). West Island is mostly bare except for scattered black greasewood and an unidentified forb. Like East Island, this island has decreased in size because of high lake water levels.

California Gulls nesting at Soda Lake are secure from human intervention because this area is "off limits" to the public.

Yellowstone Lake

Linton (1891) indicated there were many adult California Gulls present at Yellowstone Lake, Yellowstone National Park, 10 July 1890 but did not provide substantial evidence of nesting. Breeding was first reported by Skinner (1917), who estimated that 1,000 gulls were present in Yellowstone National Park and practically all nested on the Molly Islands, Yellowstone Lake, in 1898. The California Gull breeding population appeared to have varied considerably between 1917 and 1966 (Diem and Condon 1967). On 6 July 1962 Schaller (1964) estimated there were 600 active nests. Recently, numbers of California Gulls breeding on the Molly Islands have remained relatively unchanged since Schaller's census (K. L. Diem, personal communication).

The Molly Islands have been previously described (Schaller 1964, Diem and Condon 1967, Diem 1979). The two Molly Islands, Rocky Island and Sandy Island, are about 0.4 km apart and 0.8 km from the southern shore of the Southeast Arm of Yellowstone Lake (Fig. 1). The combined surface area of the islands varies between 0.3 ha and 0.5 ha depending on water levels. Both islands are sparsely vegetated. Nesting associates in 1981 included the American White Pelican (290 active nests), Double-crested Cormorant (17 active nests), and Caspian Tern (14 active nests) (K. L. Diem, personal communication).

Because of National Park Service concern for the welfare of white pelicans and other colonial waterbirds breeding on the Molly Islands, scientific investigations have been restricted and the nesting colonies are closed to the public.

DISCUSSION

According to Conover (1983), two California Gull nesting colonies existed in Wyoming in 1980; one was at Bamforth Lake, Albany County, and the other at Yellowstone Lake, Yellowstone National Park. Nesting colonies were also present at Ocean and Soda lakes but were overlooked when Conover conducted his survey. In addition, several new California Gull colonies have become established elsewhere in Wyoming in recent years (Table 1). Table 1 indicates the occurrence of approximately 7,273 nests in the state.

The construction of large reservoirs with isolated islands has created substantial nesting habitat for California Gulls in Wyoming.

TABLE 1. Location, number of nests, year of establishment, and habitat of California Gull colonies in Wyoming, 1984.

Name	Location	Year colony established	Number of nests	Habitat
ALBANY COUNTY				
Bamforth Lake				
1. Bamforth Island	41°24′N,105°44′W	1934	2,470[a]	Lake
2. Peninsula Island	41°24′N,105°44′W	1984	—	
CARBON COUNTY				
Pathfinder Reservoir				
3. Bird Island	42°23′N,106°56′W	Before 1982	683	Reservoir
FREMONT COUNTY				
Ocean Lake WHMU				
4. Peninsula Island	43°07′N,108°35′W	1983	775	Reservoir
Sand Mesa WHMU				
5. Pond No. 1	43°19′N,108°20′W	1983	162	Reservoir
NATRONA COUNTY				
Soda Lake				
6. Man-made Island	42°54′N,106°18′W	1984	1,906 ± 204[b]	Reservoir
7. Rattlesnake Island	42°54′N,106°18′W	1984	560	
8. East Island	42°54′N,106°18′W	Early 1960s	24	
9. West Island	42°54′N,106°19′W	Early 1960s	93	
YELLOWSTONE NATIONAL PARK				
Yellowstone Lake				
10. Molly Islands	44°19′N,110°16′W	Before 1898	600[c]	Lake

[a] Population estimate is from 1975 (Raper 1975).
[b] Mean ± SE.
[c] Population estimate is from 1962 (Schaller 1964).

Seven of eight California Gull nesting colonies (87%) that have become established since the 1960s are on man-made water impoundments, and two of these colonies are on man-made islands.

Although quantitative data are lacking on the diet of California Gulls in most colonies, food resources appear to have been influenced by man's activities in Wyoming. Expanded agriculture may have provided considerable food for California Gulls, especially in colonies at Ocean Lake and Sand Mesa WHMUs. Gulls from these colonies commonly forage in the extensive cultivated and irrigated fields nearby. Although gulls at Ocean Lake and Sand Mesa WHMUs also exploit refuse left by fishermen and other recreational users, minimal sign of garbage occurs in both colonies. In contrast, California Gulls at Soda Lake seem to rely heavily on food resources available at the nearby Casper garbage dump. Gulls nesting at Bamforth Lake, Pathfinder Reservoir, and Yellowstone Lake appear to have a more natural diet. Pugesek (1983) found that most California Gulls from Bamforth Lake foraged at freshwater sources within 20 km of the colony, and he observed that the diet of offspring mainly consisted of aquatic insects, salamanders, and fish. Although California Gulls from colonies in Yellowstone National Park and Pathfinder Reservoir consume refuse left by fishermen and other recreational users, their diet probably consists mostly of natural food resources since man-caused environmental changes, which would create food, have not taken place in either area.

Conover et al. (1979) indicated that decreased human predation on California Gulls and their eggs was partially responsible for the population increase in Washington State. In Wyoming, California Gulls have continued to increase despite continuous human persecution in the state.

ACKNOWLEDGMENTS

I thank Larry Pate and Lynn Jahnke for assistance with censusing gull colonies in the Casper area. Kenneth L. Diem provided recent information on the Yellowstone Lake colony. Nancy Findholt, Joseph Jehl, and Bob Oakleaf made many helpful suggestions on the manuscript. All information gathered on

California Gull colonies was made possible through funding by the Wyoming Game and Fish Department, Nongame Project.

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NEW GENUS AND SPECIES OF LEAFHOPPER IN THE TRIBE TINOBREGMINI (HOMOPTERA: CICADELLIDAE: COELIDIINAE)

M. W. Nielson[1]

ABSTRACT— A new genus, *Stenolidia*, and new species, *S. magna* (type species), are described and illustrated. *Stenolidia* from Guyana is the fifth genus in the tribe Tinobregmini and the third that has come to light since the tribe was revised in 1975.

Since the revision of the tribe Tinobregmini (Nielson 1975), two new genera, *Tantulidia* Nielson and *Corilidia* Nielson (Nielson 1979, 1982), have been described and assigned to the tribe. At this time I describe a new genus, *Stenolidia*, from Guyana and add a fifth member to the tribe that further broadens the tribal concept and distribution of the group.

The tribe Tinobregmini, sensu stricto, originally included only *Tinobregmus* Van Duzee from the southern United States. DeLong (1945) described additional species of *Tinobregmus* from Mexico; then he later (1969) described *Chilelana* from Chile and assigned it to the Tinobregmini. Narrow crowns, brachytery, and pronotal concealment of forewing bases were the primary characters that united these members of the tribe.

The recent addition of *Tantulidia* and *Corilidia* not only broadened the tribal concept but also coalesced the distributional gap between *Tinobregmus* and *Chilelana*. *Stenolidia* is placed in the tribe Tinobregmini with some reservations. Its external features are nearest to *Tantulidia*, but its aedeagal characters are closest to *Corilidia*. Therefore, it seems more appropriate to place *Stenolidia* in Tinobregmini than to erect a new tribe or relegate it to the tribe Coelidiini, to which it clearly does not belong. *Stenolidia* keys nearest to *Tantulidia* in my 1982 paper.

In addition to the aforementioned characters, the normal pronotum, scutellum, and forewings (not reduced) are now adjunct characters for the tribe. Except in *Corilidia* and *Stenolidia*, the aedeagal characters in the remaining described genera are quite diverse.

Stenolidia, n. gen.

Type-species: *Stenolidia magna*, n. sp.

Medium-sized, slender species. Similar to *Tantulidia* Nielson in general habitus but with distinctive male genital characters. Color black except for eyes and face.

Head much narrower than pronotum; crown elevated, very narrow and produced distally; eyes very large, elongate-ovoid; pronotum large, scutellum moderately large; forewing elongate, 5 apical and 3 anteapical cells present, outer one closed; hind wing well developed; clypeus long, narrow, without median longitudinal carina; clypellus long, broad at distal 1/3.

MALE. Genitalia partially asymmetrical; pygofer broad with short caudodorsal process; aedeagus asymmetrical, long with dorsal processes near middle of shaft; connective Y-shaped, stout; style moderately long; plate long, narrow with subapical constriction.

Stenolidia is known only by a single species from Guyana. It is nearest to *Tantulidia* in general habitus by not having the bases of the forewings concealed by the posterior margin of the pronotum and to *Corilidia* Nielson in certain aedeagal characters. The genus can be readily separated from these genera by the long, narrow elevated crown with parallel lateral margins and by the subapical constricted plate.

Stenolidia magna, n. sp.

Length: male 7.10 mm.

General color black except for light reddish brown eyes and deep tannish face, dark ochraceous areas in costa of forewings.

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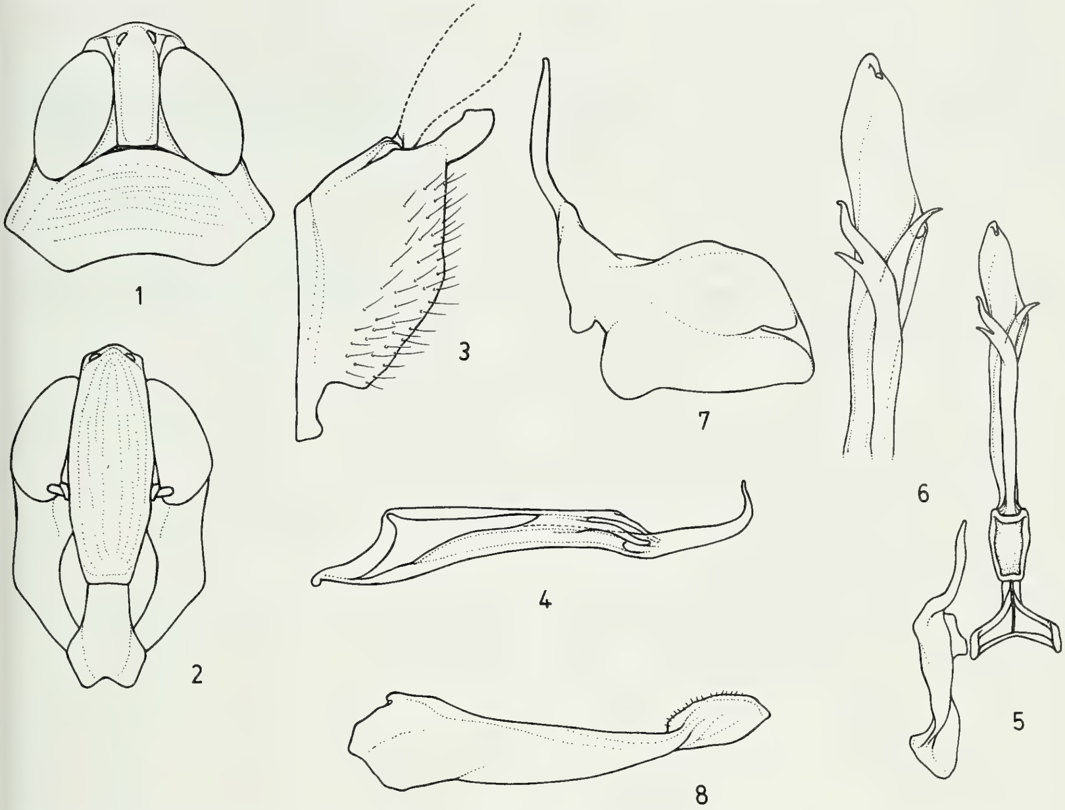

Figs. 1–8. *Stenolidia magna*, n.sp.: 1, Head and pronotum, dorsal view. 2, Face. 3, Male pygofer, lateral view. 4, Aedeagus, lateral view. 5, Connective, aedeagus and right style, dorsal view. 6, Aedeagus distal enlargement, dorsal view. 7, Style, lateral view. 8, Plate, ventral view.

Head much narrower than pronotum (Fig. 1); crown very narrow, distinctly produced distally beyond anterior margin of eyes, width nearly 1/2 width of eyes, prominently elevated above level of eyes, lateral margins parallel, slightly carinate; eyes very large, elongate-ovoid; pronotum large (atypical of tribe), length nearly equal to length of crown; scutellum moderately long; forewing elongate, appendix well developed; clypeus long and narrow, narrower anteriorly than posteriorly, surface finely rugose anteriorly; clypellus long, lateral margins broad at distal 1/3 (Fig. 2).

MALE. Pygofer broad with rectangular ovate lobe on caudodorsal margin (Fig. 3); aedeagus asymmetrical, long, broad at basal 2/3, with longitudinal transparent area along middle in lateral view (Fig. 4), compressed dorso-ventrally at distal 1/3 with apex narrowed and curved dorsally in lateral view, two stout spines arising from dorsal surface of shaft just distad of middle, the dorsal one slightly undulated with a secondary, short lateral process, ventral one single and slightly curved (Fig. 5, 6); gonopore subapical, opening near dorso-lateral margin of shaft; connective stout, Y-shape, with short stem; style short, broad basally and narrowed at distal half (Fig. 7); plate long and narrow, distinctive constriction subapically, with few microsetae apically (Fig. 8).

FEMALE. Unknown.

Holotype (male), GUYANA: New River, 750 ft, 1–5.V.1938, C. A. Hudson (BMNH).

REMARKS: *Stenolidia magna* is the only known representative of the genus and can be separated from species of other genera in the tribe by characters described above. It is the largest in size among all known species in the tribe.

ACKNOWLEDGMENTS

I express my sincere appreciation to Dr. W. J. Knight, British Museum (Natural History)

(BMNH), for loan of this specimen, to Jean Stanger for the excellent illustrations, and to Dr. James P. Kramer, U.S. National Museum, Washington, D.C., and Dr. Paul W. Oman, Oregon State University, Corvallis, for reading the manuscript.

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NEW ORIENTAL GENUS OF LEAFHOPPERS IN THE TRIBE COELIDIINI WITH DESCRIPTIONS OF NEW SPECIES (HOMOPTERA: CICADELLIDAE: COELIDIINAE)

M. W. Nielson[1]

ABSTRACT—A new genus, *Stylolidia*, and two new species, *Stylolidia pectinata* n. sp. (type species) and *Stylolidia cristata* n. sp., from Malaysia are described and illustrated. A key to the males of the known species is also included.

The Oriental leafhoppers of the tribe Coelidiini are composed of five rather distinct genera, three of which are fairly large and have speciated over the entire region (Nielson 1982). Two genera, *Mahellus* Nielson and *Jenolidia* Nielson, are small and geographically restricted. The former occupies the western edge of the Oriental region, whereas the latter is known only from Borneo.

The new genus *Stylolidia* is described from two new species, *S. pectinata* (type-species) and *S. cristata*, from Malaysia. Both species have unusual characters, i.e., tubular aedeagi without processes and styles with prominent spines, which distinguish the genus from other Oriental genera in the tribe. The styles of *S. cristata* are similar to *Lodiana unica* Nielson, but in the former each style has two rows of uniseriate spines whereas the latter has only one row.

Key to males of *Stylolidia*

1. Style with long spines arising from apex . . . . *pectinata*, n. sp.
   Style with two rows of short spines arising from inner lateral margin of apical half . . . . *cristata*, n. sp.

Stylolidia n. gen.

Type-species: *Stylolidia pectinata*, n. sp.

Medium-sized species. Length male 8.00–8.80 mm. Similar to *Lodiana* Nielson in general habitus and to *Taharana* Nielson in aedeagal characters. Color deep brown to blackish with mottled markings on forewings.

Head narrower than pronotum, subconical; crown narrow, width less than width of eye, produced slightly beyond anterior margin of eyes, nearly rounded at apex, lateral margins converging basally; pronotum and scutellum large; forewing with 5 apical cells and 3 anteapical cells, outer one closed; hind wing well developed; clypeus narrow, without median longitudinal carina; clypellus narrow at basal 2/3, expanded at apical 1/3.

MALE. Genitalia partially asymmetrical. Pygofer with or without caudodorsal process, caudoventral process absent; 10th segment long and narrow; aedeagus tubular, without processes (similar to *Taharana*); dorsal apodeme long and narrow; connective broadly Y-shaped; style long with distinctive spines; plate long, narrow with few microsetae on surface.

The genus *Stylolidia* is known only from Malaysia and is represented by the two species described below. It can be distinguished from *Lodiana* by the absence of processes on the aedeagus and from *Taharana* by the long style with spines on its distal half.

Stylolidia pectinata, n. sp.

Length: Male 8.00 mm.

Moderate-sized, slender species. General color dark brown with tannish mottled markings on forewing.

Head narrower than pronotum (Fig. 1); crown narrower than width of eye, slightly produced distally, slightly elevated above level of eyes; ocelli near anterior margin of crown; eyes large, semiglobular; pronotum, scutellum, and forewing as in description of genus; clypeus long, narrow, lateral margins broadly convex, flat medially (Fig. 2); clypellus as in description of genus.

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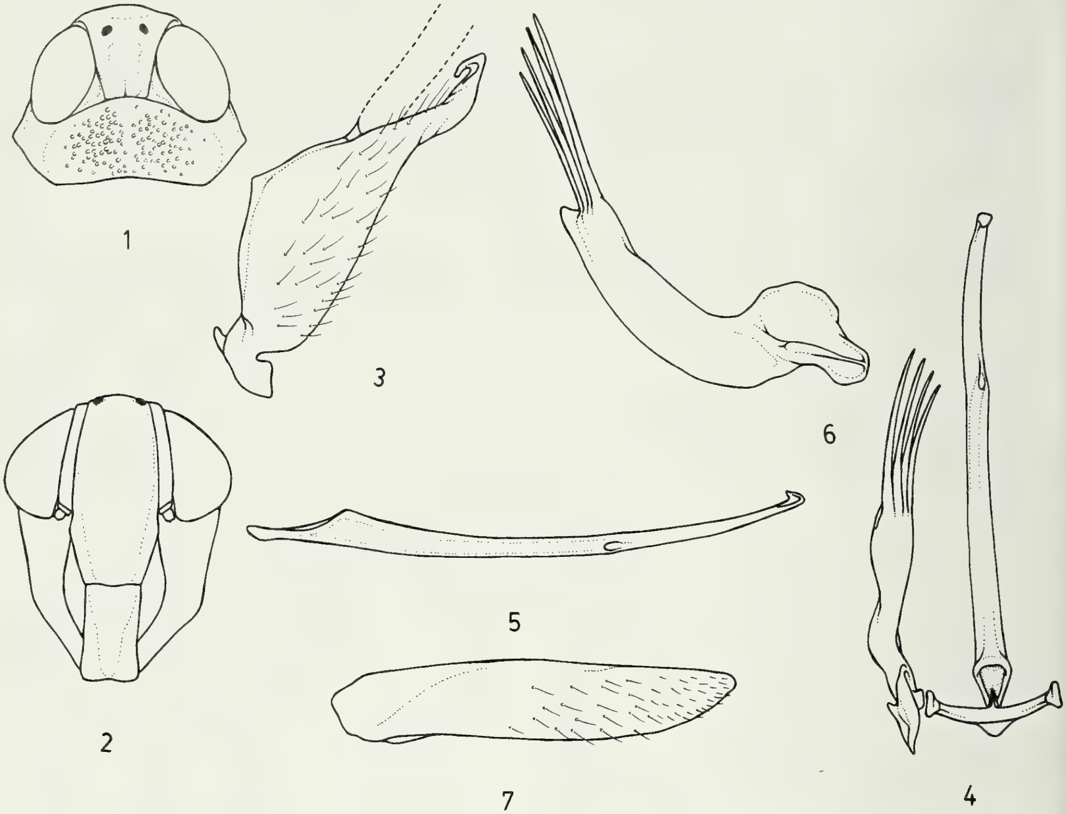


Figs. 1–7. *Stylolidia pectinata*, n. sp.: 1, Head and pronotum, dorsal view. 2, Face. 3, Male pygofer, lateral view. 4, Connective, aedeagus, and right style, dorsal view. 5, Aedeagus, lateral view. 6, Style, lateral view. 7, Plate, ventral view.

MALE. Pygofer in lateral view with hooked caudodorsal process (Fig. 3); aedeagus long, narrow, tubular, slightly curved in lateral view and extending beyond apex of style, without processes (Figs. 4, 5); gonopore distad of middle of shaft on lateroventral margin; style short, not reaching apex of aedeagal shaft, with 4–5 very long nearly straight spines arising from apex, spines nearly as long as basal half of style (Figs. 4, 6); plate long and narrow (Fig. 7).

FEMALE. Unknown.

Holotype (male), MALAYSIA: Malay Penins., Perak, 15-XI-1927, G. Kledang (BMNH).

REMARKS: S. *pectinata* is easily separated from S. *cristata* by the hooked caudodorsal process on the pygofer and by the long spines that arise from the apex of the style.

Additional data on the label attached to the holotype specimen include abbreviations "F.M.S." and "2650" on the top side and "presented by Mr. E. S. Kimund, Sel: Mus:" on the underside.

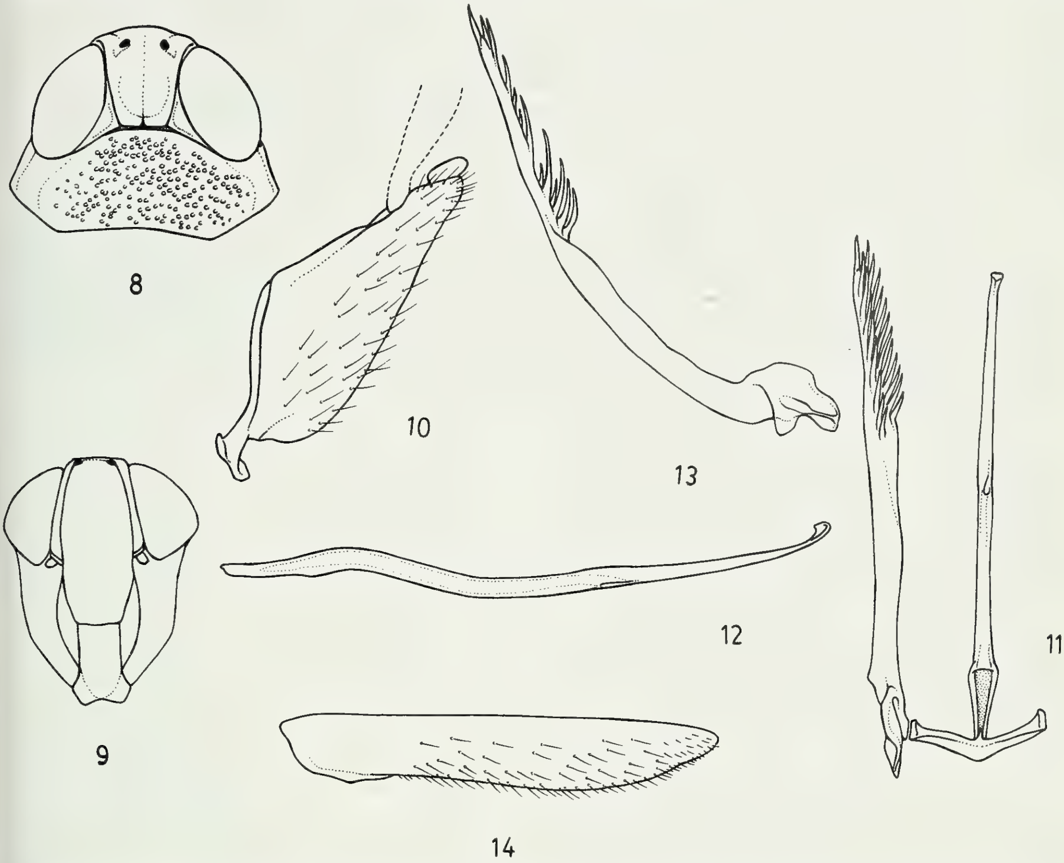
Stylolidia cristata, n. sp.

Length: Male 8.80 mm.

Medium-sized, slender species. General color blackish with numerous mottled tannish markings on forewing.

Head as in *pectinata* n. sp. but with larger semiglobular eyes (Fig. 8); pronotum, scutellum and forewing as in description of genus; clypeus and clypellus as in *pectinata* (Fig. 9).

MALE. Pygofer in lateral view with small, translucent, scalelike process on caudodorsal margin (Fig. 10); aedeagus long and tubular, without processes (Figs. 11, 12); gonopore as in *pectinata*; style very long, extending distally beyond apex of aedeagal shaft, with two rows of uniseriate stout spines on distal half, one row on dorsal margin and the other on the inner lateral margin (Figs. 11, 13); plate as in *pectinata* (Fig. 14).



Figs. 8–14. *Stylolidia cristata*, n. sp.: 8, Head and pronotum, dorsal view. 9, Face. 10, Pygofer, lateral view. 11, Connective, aedeagus, and right style, dorsal view. 12, Aedeagus, lateral view. 13, Style, lateral view. 14, Plate, ventral view.

FEMALE. Unknown.

Holotype (male) MALAYSIA: Pahang Bukit Ibam, 90 km WNW of Kuala Rompin, ca 50m 5–9. X. 1961, at night, K. J. Kuncheria (BPBM).

REMARKS: This species can be distinguished from S. *pectinata* by the long style that exceeds the length of aedeagus and by the two uniseriate rows of spines on the distal half of style.

ACKNOWLEDGMENTS

Dr. W. J. Knight, British Museum (Natural History), London (BMNH), and the late Dr. J. Linsley Gressitt, Bernice P. Bishop Museum, Honolulu (BPBM), graciously loaned the specimens on which this paper was based. Jean Stanger provided the illustrations and Dr. James P. Kramer, U. S. National Museum, Washington, D.C., and Dr. Paul W. Oman, Oregon State University, Corvallis, gave of their time to review and improve the content of the paper.

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NIELSON, M. W. 1982. A revision of the subfamily Coelidiinae (Homoptera: Cicadellidae). IV. Tribe Coelidiini. Pacific Insects Monogr. 38. 318 pp., 1,104 figs.

ECOLOGICAL DIFFERENCES OF C_3 AND C_4 PLANT SPECIES FROM CENTRAL UTAH IN HABITATS AND MINERAL COMPOSITION

C. Morden[1], Jack D. Brotherson[2], and Bruce N. Smith[2]

ABSTRACT.—Six study sites were established in each of three community life form types (grass, forb, and shrub) containing as dominants or subdominants either C_3 and/or C_4 plants. Soil and vegetation samples were analyzed for total nitrogen, phosphorus, magnesium, calcium, potassium, sodium, zinc, iron, copper, and manganese. Discriminant analysis and analysis of variance statistics were used to evaluate differences in mineral content of soils and plant tissues. C_4 plants in all study sites assimilated higher concentrations of potassium, iron, and calcium than did C_3 plants. Forbs in all sites contained the highest concentrations of minerals, followed by shrubs and grasses.

Studies have shown that 40%–50% of the soluble leaf protein in C_3 species consists of RUBPcase, whereas in C_4 species only about 5%–20% was RUBPcase (Blenkinsop and Dale 1974). Based on this evidence, Brown (1978) suggested that C_4 species should require less nitrogen than do C_3 species. Several studies have supported this hypothesis (Christie 1979, Hallock et al. 1965, Wilson and Haydock 1971, Wilson 1975). It has also been shown that C_4 species require small amounts of sodium for growth (Brownell and Crossland 1972), although these studies were done on species specifically adapted to different environments (saline vs. nonsaline). It was the purpose of this study to investigate the mineral relationships of C_3 and C_4 plant species that grow in natural communities of comparable environmental condition to assess whether ecological differences in mineral uptake do exist.

MATERIALS AND METHODS

Study Area

Thirty-six study sites were established in plant communities bordering Utah Lake, Utah County, Utah, at approximately 40°10′ N, 11°50′ W (Fig. 1). Elevations ranged from 1,368 to 1,408 m above sea level, with a mean of 1,377 m. Six study sites were established in each of six community types. Communities were selected because of the presence of the species *Sporobolus airoides, Puccinellia nuttalliana, Atriplex patula, Kochia scoparia, Sarcobatus vermiculatus*, and *Atriplex confertifolia*. These species represent three life forms (grass, forb, and shrub), with each life

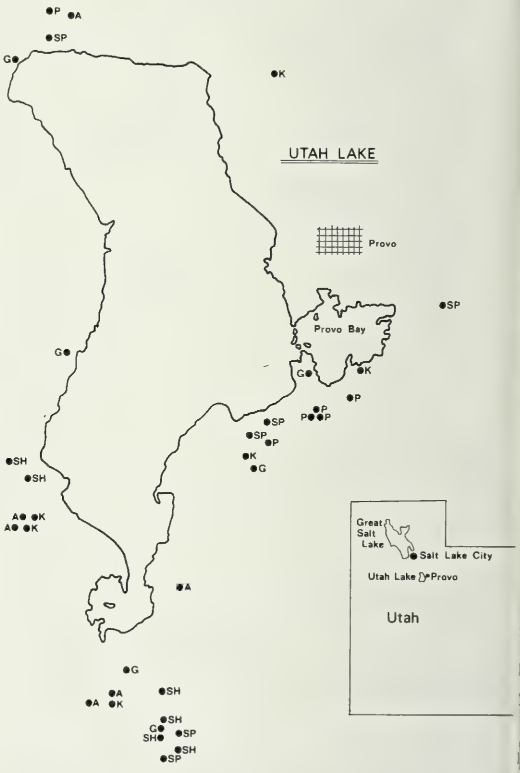

Fig. 1. A map of Utah Lake showing the locations of study sites around the lake. Communities shown correspond to P = *Puccinellia*, Sp = *Sporobolus*, A = *Atriplex*, K = *Kochia*, G = Greasewood and Sh = Shadscale.

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TABLE 1. Species along with their mean cover values and life form designation. An asterisk (*) indicates C_4 species, and the letters indicate life form type (i.e., g = grass; f = forb; s = shrub).

1. C_4 grass sites	*% cover*	2. C_3 grass sites	*% cover*
Allenrolfia occidentalis - s**	2.5	*Bromus tectorum* - g	2.6
Atriplex patula - f	4.3	*Cardaria draba* - f	1.0
**Distichlis spicata* - g	30.7	*Circium undulatum* - f	1.9
Hordeum jubatum - g	3.9	**Distichlis spicata* - g	7.0
Juncus balticus - g	2.2	*Hutchinsia procumbens* - f	1.6
**Kochia scoparia* - f	1.8	*Iva axillaris* - f	5.8
Lepidium perfoliatium - f	1.1	*Juncus balticus* - g	1.0
Polygonum ramosissimum - f	1.3	**Kochia scoparia* - f	9.4
Puccinellia nuttalliana - g	34.1	*Poa pratensis* - g	2.4
Salicornia rubra - f	4.1	**Sporobolus airoides* - g	55.5
Suaeda depressa - f	11.9	*Suaeda depressa* - f	1.5
3. C_4 forb sites	*% cover*	4. C_3 forb sites	*% cover*
Ambrosia artimisiifolia - f	2.1	*Bromus tectorum* - g	8.3
Atriplex patula - f	44.9	*Descurainia sophia* - f	4.2
Bromus tectorum - g	2.2	**Distichlis spicata* - g	1.3
**Distichlis spicata* - g	5.1	*Echinochloa crusgalli* - g	2.6
Echinochloa crusgalli - g	2.4	**Kochia scoparia* - f	60.7
Eleocharis macrostachya - g	1.2	*Lepidium perfoliatum* - f	14.5
Hordeum jubatum - g	5.8	*Puccinellia nuttalliana* - g	1.2
**Kochia scoparia* - f	1.3	*Ranunculus testiculatus* - f	1.3
Lactuca scariola - f	1.4		
Populus alba - s	15.6		
Salix amygdaloides - s	7.9		
Xanthium strumarium - f	4.4		
5. C_4 shrub sites	*% cover*	6. C_3 shrub sites	*% cover*
Bromus tectorum - g	33.2	**Atriplex confertifolia* - s	12.1
Cardaria draba - f	3.1	*Bromus tectorum* - g	7.9
Descurainia sophia - f	1.9	*Kochia americana* - f	3.8
Erysimum repandum - f	3.5	*Lepidium perfoliatum* - f	8.2
Lepidium perfoliatum - f	3.4	*Ranunculus testiculatus* - f	57.4
Ranunculus testiculatus - f	16.2	*Sarcobatus vermiculatus* - s	1.3
**Salsola iberica* - f	2.5	*Sitanion hystrix* - g	1.5
Sarcobatus vermiculatus - s	23.5	*Suaeda fruticosa* - f	1.3
Sitanion hystrix - g	1.0	*Tetradymia spinosa* - s	1.0
**Sporobolus airoides* - g	2.6		

form represented by both C_3 and C_4 species (Table 1). Taxonomic references follow Cronquist et al. (1977) for the grasses and Welsh and Moore (1973) for the dicots.

Weather data for Provo, Utah, is representative of the study area. The average annual precipitation is 340 mm, with 60% of the total falling in the winter and spring months. The hottest month of the year is July, averaging 33 C; the coldest month is January, averaging 3 C. Tributary streams from the Uintah and Wasatch mountain ranges directly east of Utah Lake provide the majority of its water. Precipitation in these mountains ranges from 760 to 1,270 mm annually (Swenson et al. 1972).

Field Methods

The study sites were selected to depict representative samples of the six community types in the Utah Lake area (Fig. 1). A 10 x 10 m study plot (0.01 ha) was established at each site. Variation in slope, drainage, erosion, and exposure was kept to a minimum. Plots were delineated by a cord 40.0 m long with loops every 10 m for corners. The corners were secured by steel stakes. Twenty 0.25 m^2 quadrats were placed at regular intervals within the study plot. Density and frequency of all plant species encountered were determined from the quadrat data. Cover values were estimated as suggested by Daubenmire (1959). Only those species showing 1% or more of the total cover are included in the analysis.

Christie (1979) found that the top layer of soil is the region of most active mineral uptake. Therefore, soil samples (an 8 cm core) were taken from the top 20 cm of soil in each study plot from opposite corners and the center. Samples were pooled and then analyzed for texture (Bouyoucos 1951), pH, soluble salts, and mineral content. The hydrogen ion concentration was measured with a glass electrode pH meter. Total soluble salts were determined with a Beckman electrical conductivity bridge. A paste consisting of a 1:1 g/v soil to water (distilled) mixture was used in determining pH and soluble salts.

Vegetation samples were obtained by taking selected clippings of herbaceous material from the C_3 species (*Sporobolus airoides*, *Kochia scoparia*, and *Atriplex confertifolia*) and the C_4 species (*Puccinellia nuttalliana*, *Atriplex patula*, and *Sarcobatus vermiculatus*) within the study plots. Soil and vegetation samples (new growth leaves) were analyzed for total nitrogen, magnesium, calcium, potassium, sodium (Hesse 1971), zinc, iron, copper, and manganese (Lindsay and Norvell, 1969). Discriminant analysis (Klecka 1975) and analysis of variance (Ott 1977) were used to statistically determine differences in mineral content between C_3 and C_4 species and their habitats.

Discriminant analyses were conducted using the Statistical Package for the Social Sciences (SPSS) computer program (Klecka 1975). This technique distinguishes statistically between two or more groups of stands on the basis of discriminating variables. The groups and variables are selected by the researcher. All variables measured can be used in the analysis (direct method), or a stepwise method can be used to reduce the number of variables to those that provide the best discriminating power among the groups. In this study both the direct and the Wilks stepwise methods were used. The Wilks method uses the overall multivariate F ratio to test for variable differences. It selects the variables independently for entry into the analysis based on the importance of their discriminating power.

The analysis procedure combines the discriminating variables to create discriminant functions designed to provide maximum separation among the groups previously specified (life forms and C_3 and C_4 photosynthetic types). The discriminant program determines the relative percentage of the total variation in the discriminating variables that is accounted for in each function. It also determines the relative importance of each variable used to create the discriminant functions. This information can be used to identify the variables having the greatest influence on the outcome of the analysis.

A graphic representation of the results of discriminant analysis is possible if the discriminant functions are viewed as axes in geometric space. A plot of stands based on the two most important functions locates the stands in

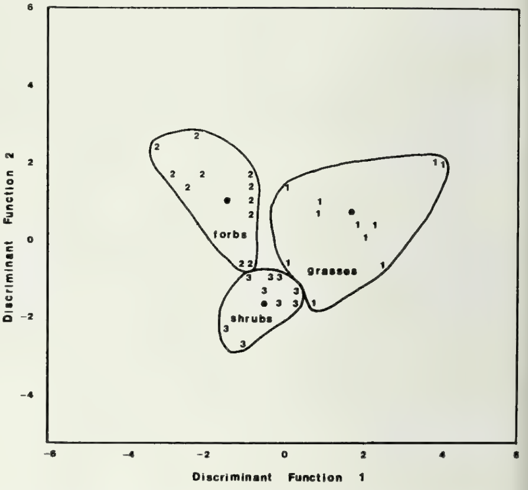

Fig. 2. Discriminant analysis for soil minerals. Of the groups, 83% were classified correctly. Numbers refer to grasses (1), forbs (2), and shrubs (3).

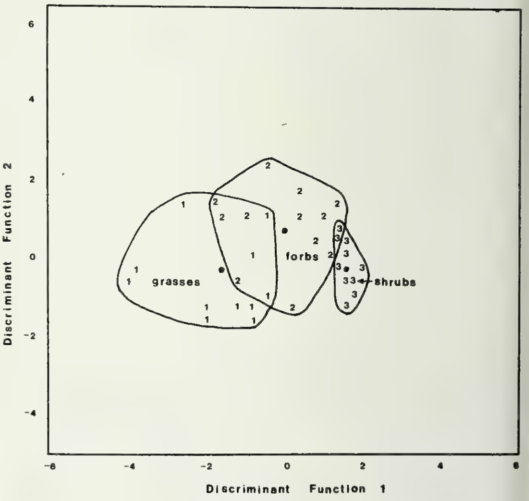

Fig. 3. Discriminant analysis for soil chemistry and texture. Of the groups, 78% were classified correctly. Numbers refer to grasses (1), forbs (2) and shrubs(3).

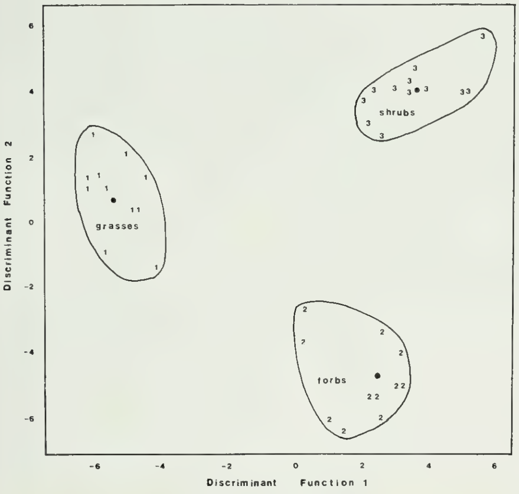

Fig. 4. Discriminant analysis for vegetation (leaf) minerals. Of the groups, 100% were classified correctly. Numbers refer to grasses (1), forbs (2), and shrubs (3).

two-dimensional space in such a way that the relationships among the groups can be visualized. Such a graphic representation is especially important for assessing the amount of separation between one group and another as well as the degree of group overlap.

RESULTS

Results of cover analysis for our study sites are given in Table 1. Only those species showing 1% or more of the total cover are included. In the grass- and forb-dominated communities, *Sporobolus airoides*, and *Kochia scoparia* provided over half the total cover. The shrub communities, however, were dominated in their understory by the invader species *Bromus tectorum* L. and *Ranunculus testiculatus* Cranz. Their presence in the understory is indicative of site disturbance as a result of grazing.

Hydrogen ion concentration showed no significant differences between the communities. All soils were basic, with a pH ranging from 8.1 to 8.7. Soil texture also showed no significant differences between communities, all of them being clay to silty clay loams. Soluble salts were highest in the grass communities and lowest in the shrub communities.

Two-dimensional plots of discriminant analysis of the mineral content of vegetation and soil samples within each life form (grasses, forbs, and shrubs) were made. The percent of grouped cases classified correctly were 83% for the soil materials (Fig. 2) and 78% for soil chemistry and texture (Fig. 3), whereas the mineral content of the vegetation classified the groups 100% correctly (Fig. 4). This indicates that habitat differences in soil mineral chemistry and texture influence the life form type that dominates a site and that differential partitioning of the minerals by the plants occurs to a great extent. The soil, of course, may also be modified by the plants growing in it.

Results of analysis of variance and Newman-Kuel tests for parameters of soil and vegetation mineral content are given in Tables 2 and 3. Analysis of soil mineral content showed significant differences between means for manganese, sodium, and soluble salts. Analysis of vegetation mineral content showed differences between life forms in nitrogen, phosphorus, zinc, manganese, copper, magnesium, potassium, and sodium.

C_3 and C_4 species were 78% correctly classified by minerals for both soil and vegetation samples (Tables 2 and 3). Stem and leaf plots of the discriminant analyses based on soil and vegetation mineral content are given in Figures 5 and 6, respectively.

Results of the analysis of variance between C_3 and C_4 species are shown in Table 4. Iron and manganese are significantly ($p < .05$) higher in concentrations in the soils of C_3-dominated species than of C_4-dominated species. However, concentration of these minerals within the plant tissue is not significantly different. Calcium and potassium showed no significant differences in concentration in soils but were significantly different in the plant tissues of C_3 and C_4 species. Plant:soil ratios were computed for each mineral. Mean differences in iron and sodium assimilation exist between C_3 and C_4 species. Although trends existed for other elements, differences between C_3 and C_4 species were not significant.

DISCUSSION

Brown (1978) suggested that differences in nitrogen use between photosynthetic types (C_3 vs. C_4) would hold for grasses, but he was not sure of the results that might be obtained with respect to other life forms. It appears

TABLE 2. Differences in the mineral concentrations of soils associated with the life forms as determined by analysis of variance and Newman-Keul tests. Means with similar letters following indicate no significant differences for those means. Those with different letters indicate significant differences.

	Nutrient concentrations in life form soils			Level of
Mineral	Grasses	Forbs	Shrubs	significance
	mg/Kg			
Nitrogen	2023a ± 1105	2026a ± 1088	1106a ± 284	NS
Manganese	10.3ab ± 8.87	15.3b ± 8.51	7.1a ± 2.3	.05
Calcium	15287b ± 5195	11231a ± 2804	10368a ± 1497	.05
Magnesium	2002a ± 1168	1260ab ± 1309	748b ± 421	.05
Sodium	3428b ± 2086	1233a ± 1065	474a ± 209	.01
Salt	7470a ± 5712	3251ab ± 2506	639b ± 440	.05

TABLE 3. Differences in the mineral concentrations of plant material (leaves) by life form. Differences determined by analysis of variance and Newman-Keul tests. Means with similar letters following indicate no significant differences for those means. Those with different letters indicate significant differences.

	Nutrient concentrations in life forms			Level of
Mineral	Grasses	Forbs	Shrubs	significance
	mg/Kg			
Nitrogen	9908a ±3366	22033b ± 3614	16283b ± 4220	.01
Phosphorus	943a ± 507	2471b ± 608	976a ± 244	.01
Zinc	18.8a ± 8.4	33.1b ± 15.4	12.5a ± 3.06	.01
Magnesium	2903a ±2091	7285b ± 2414	3308a ± 1519	.01
Copper	10.2ab ± 3.1	13.5b ± 3.0	8.3a ± 1.2	.01
Manganese	50.9a ± 28.1	89.6b ± 48.1	72.8ab ± 47.8	.01
Potassium	4264a ±1916	20183b ± 7911	24175b ± 5472	.01
Sodium	3060a ±1467	29079b ±16199	51967b ± 9060	.01

from our data that differences do exist in mineral uptake for the different life forms.

Nitrogen content in the plant tissue of C_3 and C_4 species showed no significant differences. These findings are contrary to the results of Christie (1979) and Hallock et al. (1965) and the hypothesis of Brown (1978). In fact, the C_4 shrub *A. confertifolia* showed less

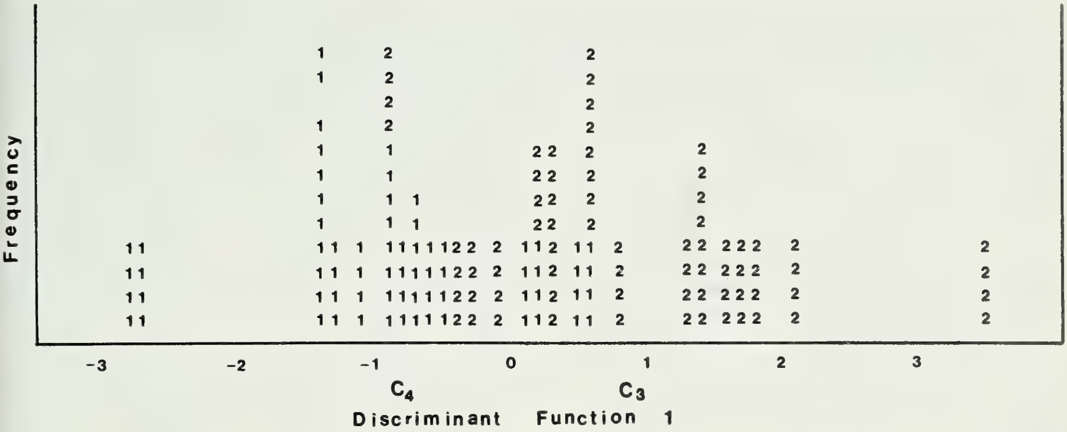

Fig. 5. Histogram of discriminant analysis for soil minerals. 1 = C_4 dominated habitats, 2 = C_3 dominated habitats.

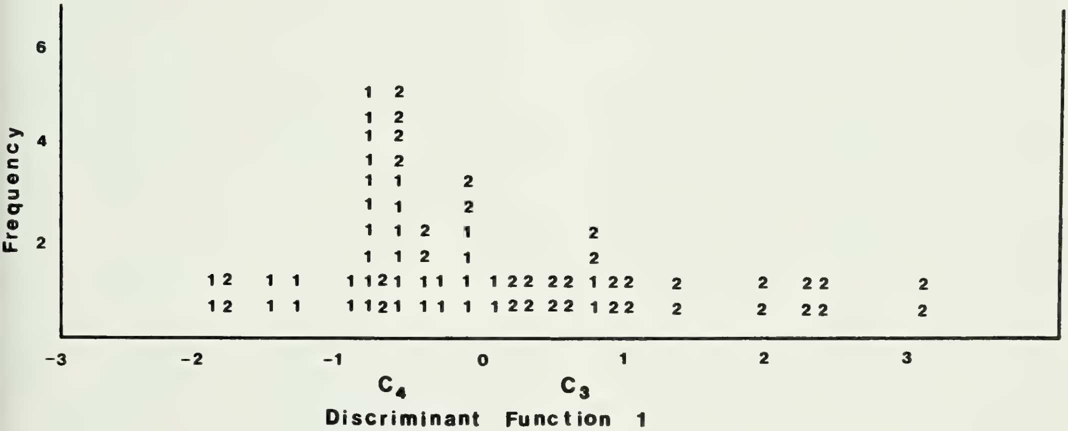

Fig. 6. Histogram of discriminant analysis for vegetation (leaf) minerals. 1 = C_4 − species, 2 = C_3 − species.

nitrogen than the C_3 shrub *S. vermiculatus*. The effect of species being adapted to similar habitats may influence this phenomenon and needs to be further investigated.

The C_3 species of this study were growing in soils significantly higher in iron content than the C_4 species (Table 4), yet no significant differences in iron and manganese concentration of the vegetation was noted. This may be due to some attribute of C_4 plants that allows them to live in soils deficient in iron and still assimilate enough for existence. It could also be due to iron being present in luxury quantities in both habitat soils and the plants assimilating iron without any restrictions. Results of this study also showed calcium to be significantly higher in C_4 vegetation than C_3 vegetation (Table 4). Concentrations of calcium in the soil of both community types is not significantly different, indicating differential uptake of calcium by the species possessing the different photosynthetic pathways. Also the C_4 species in this study assimilated significantly higher quantities of potassium than did C_3 species ($P < .005$). This is in contrast to the results obtained by Hallock et al. (1965).

Sodium may be essential as a micronutrient for C_4 species based upon studies of halophytic C_4 species and nonhalophyte C_3 species (Brownell and Crossland 1972). These workers showed that the C_4 species they studied developed lesions and some species would not flower in the absence of sodium, whereas the C_3 species grew normally. However, our field results indicate that C_4 plants do not necessarily require sodium, but that high

TABLE 4. Summary of mineral concentrations for vegetation and soil data. Means are for vegetation, soil, and plant:soil ratios for C_3 and C_4 plants across all 36 study sites. Significant differences are indicated by the presence of an asterisk (*) next to the means values. One asterisk indicates $p < 0.05$; two asterisks indicate $p < 0.01$.

	mg/Kg					
	Vegetation		Soil		Plant:soil ratio	
	C_3	C_4	C_3	C_4	C_3	C_4
N	16127.0	16022.0	1667.0	1771.0	15.3	10.6
	± 6910.0	± 5611.0	± 1198.0	± 751.0	±15.2	± 4.9
P	1489.0	1438.0	47.0	29.0	79.7	79.0
	± 825.0	± 915.0	± 104.9	± 32.3	±49.2	±54.0
Zn	22.8	21.0	3.5	1.8	18.0	21.3
	± 15.1	± 11.4	± 6.6	± 2.0	±11.5	±13.9
Fe	269.0	349.0	16.1*	6.5*	28.1	60.3
	± 220.8	± 504.0	± 14.4	± 5.1	±27.0	±63.3
Mn	82.9	59.4	14.4	7.4	9.5	8.6
	± 37.0	± 48.6	± 9.3	± 3.7	± 9.6	± 5.7
Cu	10.2	11.1	2.5	1.5	5.4	8.5
	± 3.6	± 3.2	± 1.5	± .6	± 3.1	± 3.5
Ca	10089.0*	13017.0*	12306.9	12644.0	0.9	2.0
	± 4301.0	± 5875.0	± 3852.7	± 4609.7	± 0.4	± 1.3
Mg	4390.0	4602.0	1457.0	1217.0	4.6	5.5
	± 3420.0	± 2162.0	± 1227.5	± 848.2	± 4.1	± 5.0
K	13433.0**	18965.0**	1022.0	1370.0	19.6	16.4
	± 8274.0	±11589.0	± 952.4	± 889.1	±21.0	±19.5
Na	30778.0	25292.0	1766.0	1658.0	76.8	42.7
	±22431.0	±23463.0	± 1750.7	± 1995.9	±88.1	±53.3
Salt			3921.0	3653.0		
			± 5083.0	± 4025.0		
pH			8.3	8.3		
			± 0.5	± 0.3		
Clay			33.4	30.8		
			± 13.0	± 15.3		
Silt			46.3	47.6		
			± 16.3	± 17.8		
Sand			20.2	21.7		
			± 11.8	± 15.5		

sodium uptake is characteristic of plants adapted to the saline habitat (Table 4).

Salinity would have the same effect on plant-water relations as increasing plant drought: the more salt present in a soil, the wetter the soil must be to dilute the salt and prevent salt hindrance to growth (Donahue et al. 1977). Plants possessing the C_4 photosynthetic pathway typically have a higher water use efficiency than plants possessing the C_3 pathway, which would aid in survival of the plant in semiarid regions (Ludlow 1976). C_4 plants may have a competitive advantage in saline environments due to their high water-use efficiency. Although no significant differences between salt or sodium levels in the two habitat types and in the C_3 and C_4 plants were observed, it is important to note that the C_3

species of this study had slightly higher mean levels of sodium in their tissues and higher plant:soil ratios than the C_4 species. The C_3 species also flowered one to two months earlier in the summer, when moisture conditions in the habitat were more conducive to their growth.

though grasses grew in soils with high concentrations of soluble salts (Table 2), their tissue concentrations of sodium and potassium (Table 3) were much lower than either forbs or shrubs. Although many grasses adapted to saline environments possess salt glands (Liphschitz et al. 1974, Hansen et al. 1976), *Puccinellia nuttalliana* and *Sporobolus airoides* do not and as a result must restrict the amount of sodium and potassium entering their tissues. On the other hand, the shrubs and forbs of this study do possess salt glands or become succulent (Luttge 1971) and thus are able to tolerate higher quantities of sodium and potassium in their tissues.

Both growth form and photosynthetic type showed habitat differences relative to mineral uptake. The detailed physiological basis for these differences must now be further investigated.

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RESPONSE OF WINTERFAT (*CERATOIDES LANATA*) COMMUNITIES TO RELEASE FROM GRAZING PRESSURE

Lars L. Rasmussen[1] and Jack D. Brotherson[2]

ABSTRACT.—Sixteen study sites were established in grazed and ungrazed stands of winterfat in Kane County, Utah. The area is located within the winter range of cattle and along U.S. Highway 89 between Kanab, Utah, and Page, Arizona. Road construction in 1957 dissected several winterfat communities, and following fencing part of the communities were released from grazing. Differences in species composition, vegetation, and soil characteristics between grazed and ungrazed sites were assessed. Major differences in site characteristics appeared due to the influence of winter grazing by cattle. Winterfat and Indian ricegrass showed increased cover on the nongrazed sites following release from grazing pressure. Winterfat also showed significant negative interspecific association patterns with all major species.

Winterfat (*Ceratoides lanata* [Pursh] J. T. Howell) is considered a valuable forage component of winter ranges throughout western North America. Blauer et al. (1976) described winterfat as "superior nutritious browse for livestock and big game." Griffiths (1910) pointed out that winterfat is "very much injured by overgrazing." However, more recent research has provided somewhat conflicting information relative to the tolerance of winterfat to grazing pressure. Holmgren and Hutchings (1971) indicated that percent plant cover represented by winterfat sharply declines under heavy grazing during late winter.

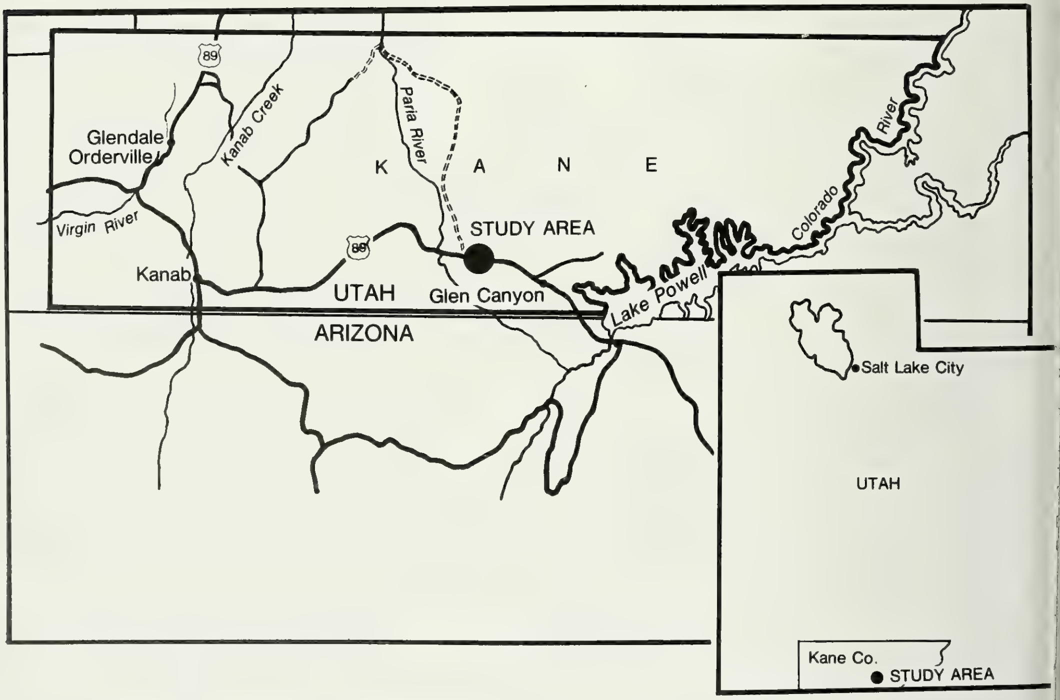

Fig. 1. Map of study site location in Kane County, Utah.

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TABLE 1. Means and standard deviations (SD) of soil factors and significance levels for the difference between the means for the grazed and nongrazed winterfat populations in Kane County, Utah. Significance levels were computed by using the student's t-statistic.

SITE FACTOR	GRAZED		UNGRAZED	
	Mean	SD	Mean	SD
Sand (%)	83.8	2.42	83.1	2.94
Silt (%)*	8.2	1.12	9.2	0.83
Clay (%)	8.6	2.47	7.6	2.98
Organic matter (%)*	0.3	0.05	0.2	0.05
pH	8.0	0.05	7.8	0.05
EC × 10^3	0.5	0.05	0.6	0.36
CEC (meq/100 g)	8.6	1.31	8.8	1.32
Calcium (ppm)*	5194.0	768.0	4375.0	1040.0
Magnesium (ppm)	109.5	32.6	177.0	26.5
Sodium (ppm)	13.3	6.26	25.6	47.3
Potassium (ppm)	226.9	45.1	264.8	90.8
Iron (ppm)	1.4	0.24	1.3	0.11
Manganese (ppm)	2.7	0.57	2.6	0.35
Zinc (ppm)	0.6	0.27	0.6	0.21
Copper (ppm)	0.4	0.05	0.4	0.07
Phosphorus (ppm)	31.0	5.31	37.0	8.44

*Significant difference between means at .05 level.

Trlica and Cook (1971) showed that winterfat did not make good growth recovery under any defoliation treatment. Yet, Norton (1978) states that winterfat is "relatively indifferent to heavy grazing."

The purpose of the present study was to examine changes in winterfat communities following 26 years of release from grazing pressure on ranges in Kane County, Utah.

STUDY AREA

U.S. Highway 89 from Kanab, Utah, to Page, Arizona, was constructed during 1957, and the right-of-way was fenced. This construction dissected winterfat communities 5 km east of the Paria River, creating grazed and ungrazed units (Fig. 1).

The area is located within the Bureau of Land Management East Clark Bench allotment. This allotment has been utilized primarily as winter range for cattle since 1956. Although entry and removal dates for livestock have varied, 1 November to 31 May was the general season of use until 1964, when the removal date for livestock was moved back to April 30.

The climatic conditions of the study area are similar to conditions at Glen Canyon City, Utah, 15 km east along U.S. 89. Average annual precipitation in the area varies from 15 to 20 cm. There are two main periods of precipitation, one beginning in December and ending in March in the form of snow and the second beginning in August and ending in October in the form of rain (Green et al. 1981). The hottest month of the year is July, with an average temperature of 28 C. The coldest month is January, with an average temperature of 0 C. The frost-free period for the area begins in late April and ends in late October, averaging 190 days (U.S. Environmental Data Service 1968).

METHODS

Sixteen stands were sampled during June and July 1984 (eight each within grazed and ungrazed sites), and data were collected to represent conditions within grazed and ungrazed winterfat communities. Each stand was subsampled, with a total of 11 1-m^2 quadrats placed one every 3 m along 33-m transect lines. Transects within the protected sites were placed parallel to and equidistant between the fence line and U.S. Highway 89. Transects within the grazed sites were placed parallel to transects in protected sites and at equal distances from the fence line.

Total living cover of vascular plants was estimated in each quadrat. Cover by life forms, soil cryptogams, litter, exposed rock, bare ground, and individual plant species were estimated using Daubenmire's cover classes (1959).

Three soil samples were taken at 10-m intervals along each transect line from the top 20 cm of soil. The three samples were later combined

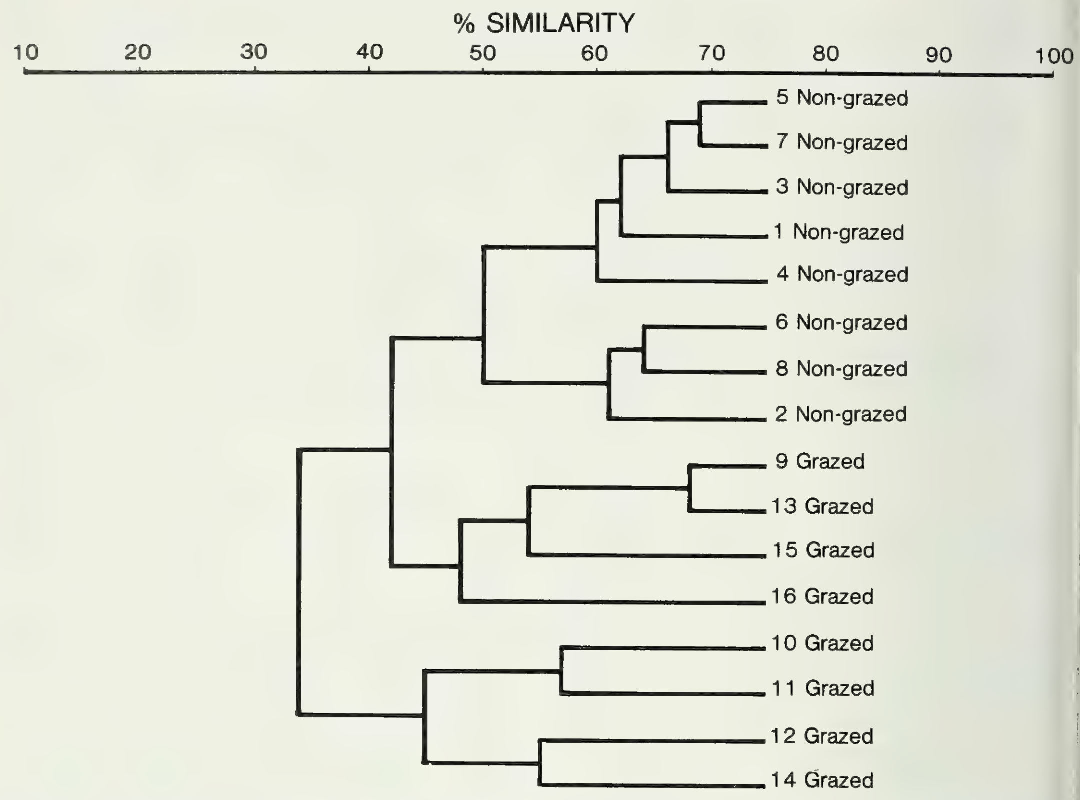

Fig. 2. Cluster dendrogram of grazed and nongrazed winterfat stands in Kane County, Utah. Cluster is based on similarity of plant species cover in site vegetation.

for laboratory analysis. Ludwig (1969) found that the surface decimeter of soil yields 80% of the information useful in correlating plant response with concentrations of essential mineral nutrients in the soil. Holmgren and Brewster (1972) showed that greater than 50% of the fine roots of plants (which included winterfat) in Utah desert communities are found in the top 15 cm of soil profile.

Soil samples were analyzed for texture (Bouyoucos 1951), pH, soluble salts, mineral composition and organic matter. Soil pH was determined with a glass electrode pH meter. Soluble salts were determined with a Beckman electrical conductivity bridge. Exchangeable calcium, magnesium, potassium, and sodium were extracted from soils with DTPA (diethylene triamine-penta-acetic acid; Lindsay and Norvell 1969). A Perkin Elmer Model 403 atomic absorption spectrophotometer was used to determine individual ion concentrations (Isaac and Kerber 1971). Phosphorus was extracted with sodium bicarbonate (Olsen et al. 1954). Organic matter wa estimated from total carbon using method described by Allison (1965).

Similarity indices comparing each stand t all other stands were calculated (Ruzick 1958). These indicies were then employed t cluster winterfat stands following Sneath an Sokal (1973). Individual plant species wer also clustered on the basis of niche overla (Colwell and Futuyma 1971). Interspecific association patterns between plant species wer computed using Cole's (1949) Index. Mean and standard deviations were computed for al biotic and abiotic variables across the 1 stands. Prevalent species were selected o the basis of cover values (Warner and Harpe 1972). Diversity indices were computed following Shannon and Weaver (1949) an McArthur (1972.) Statistical differences between grazed and ungrazed sites were calculated using Student's t-statistic.

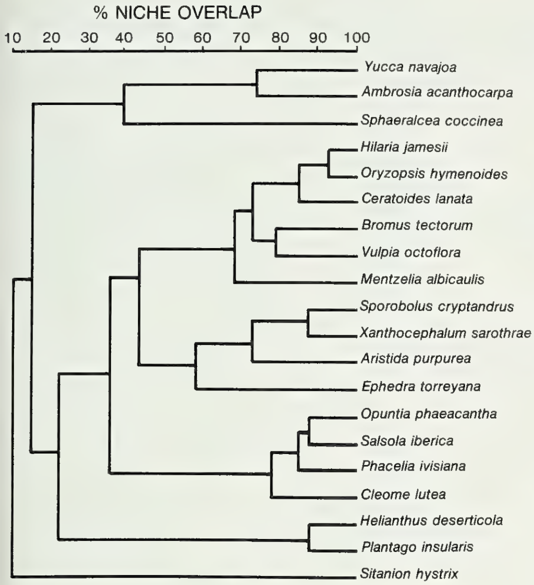
% NICHE OVERLAP
10 20 30 40 50 60 70 80 90 100
Yucca navajoa
Ambrosia acanthocarpa
Sphaeralcea coccinea
Hilaria jamesii
Oryzopsis hymenoides
Ceratoides lanata
Bromus tectorum
Vulpia octoflora
Mentzelia albicaulis
Sporobolus cryptandrus
Xanthocephalum sarothrae
Aristida purpurea
Ephedra torreyana
Opuntia phaeacantha
Salsola iberica
Phacelia ivisiana
Cleome lutea
Helianthus deserticola
Plantago insularis
Sitanion hystrix

Fig. 3. Cluster dendrogram of plant species occurring in the study area. Cluster based on niche overlap relative to a species geographical distribution.

Results and Discussion

There were few differences in edaphic factors between grazed and ungrazed winterfat communities (Table 1). Significant differences between means were observed for percent silt, percent organic matter, and calcium concentrations. The higher levels of silt in the ungrazed area are probably due to the presence of the fence. The fence (net wire) would act as a barrier to blowing weeds and plant material and thus as a barrier to drifting soil. The more-abundant vegetation on the ungrazed sites would also create a barrier against which windblown silt would tend to accumulate. The differences in percent organic matter are also probably a function of increased vegetation cover. Mean differences in these three factors are relatively small, and floristic differences between grazed and ungrazed stands are, therefore, not considered to be caused by these soil characteristics.

Cluster analysis (based on vegetative similarity) clearly separated the grazed and ungrazed transects into two groups (Figs. 2 and 3). This separation reflects the effects of long periods of winter livestock grazing on vegetative composition. Grazing-induced change is also indicated by greater diversity within the grazed stands (Table 2). The greater plant diversities observed among grazed winterfat stands is expected. Cox (1976) noted that Charles Darwin observed greater diversity within grazed lands when compared with nongrazed lands (Cox et al. 1976). Harper (1977) also indicates that the great floristic diversity within the Chalk grasslands of Britain owes its existence to the selective grazing of livestock on potentially dominant plant species. Further research may better establish the occurrence of this phenomenon on other western ranges.

A major difference between grazed and ungrazed winterfat communities was in shrub cover (Table 2). Total live cover and litter cover were also greater on the ungrazed areas. Differences in community response to release from grazing pressure is best shown by differences in species cover (Table 3). The cover of winterfat on ungrazed areas was significantly greater than on grazed areas. Greater shrub cover on the ungrazed stands was entirely accounted for by the increased cover of winterfat. Although winterfat has been described as being relatively tolerant to grazing and as a "good natural increasor" (Blauer et al. 1976), it demonstrates little tolerance to winter use by cattle on our study sites, where it was potentially the dominant shrub.

Wide ecotypic variation is known to exist between winterfat populations (Stevens et al. 1977). Populations examined in this study were characterized by relatively large plants (up to three feet in height) with a growth form similar to big sagebrush (*Artemisia tridentata*). The genetic differences of this ecotype may account in part for its susceptibility to grazing.

Cover of cool-season grasses on the ungrazed sites was greater than on grazed sites, with the cover values of Indian ricegrass (*Oryzopsis hymenoides*) showing the greatest difference. This difference was probably due to grazing pressure during the late winter season when Indian ricegrass actively grows. Grazing while the grass is actively growing would stress the plant and reduce its capacity to compete. The warm-season grass species, galleta (*Hilaria jamesii*), which does not actively grow during the late winter grazing season, maintained nearly equivalent cover values be-

TABLE 2. Means and standard deviations (SD) of site factors and significance levels for the difference between the means for the grazed and nongrazed winterfat populations in Kane County, Utah. Significance levels were computed using the student's t-statistic.

SITE FACTOR	GRAZED		UNGRAZED		SIGNIFICANCE LEVEL
	Mean	SD	Mean	SD	
Total life cover (%)	29.3	4.74	32.6	4.14	0.10
Exposed rock (%)	0.1	0.18	0.1	0.18	NS
Bare soil (%)	24.9	3.67	25.1	5.95	NS
Litter cover (%)	15.2	8.38	26.1	4.81	0.005
Cryptogram cover (%)	40.5	9.72	34.7	8.66	NS
Shrub cover (%)	7.2	3.18	13.4	4.25	0.10
Perennial grass cover (%)	20.4	7.21	18.8	8.21	NS
Annual grass cover (%)	4.2	3.26	5.1	3.79	NS
Perennial forb cover (%)	0.3	0.54	0.1	0.25	NS
Annual forb cover (%)	3.6	4.85	1.3	1.23	NS
Diversity:					
Shannon-Weaver	3.3	0.4	2.2	0.5	0.10
MacArthur	4.8	1.2	3.7	1.4	0.10

TABLE 3. Means and standard deviations (SD) of plant species cover occurring in grazed and nongrazed winterfat communities in Kane County, Utah.

SPECIES	GRAZED		UNGRAZED	
	Mean	SD	Mean	SD
Ambrosia acanthocarpa	0.1	0.09	0	
Aristida purpurea	1.6	1.47	0.3	0.95
Bromus tectorum	0.4	0.48	0.7	1.11
Ceratoides lanata	2.3	1.44	13.9	4.83
Cleome lutea	0.1	0.09	0	
Ephedra torryana	1.0	2.24	0	
Helianthus deserticola	0.1	0.31	T	
Hilaria jamesii	15.9	8.07	16.1	6.47
Mentzelia albicaulis	1.0	1.20	1.1	1.19
Opuntia phaeacantha	0.2	0.49	0	
Oryzopsis hymenoides	6.7	2.88	10.5	4.21
Phacilia ivesiana	0.1	0.03	0.1	0.03
Plantago insularis	0.3	0.81	0.1	0.14
Salsola iberica	2.4	4.13	0.2	0.49
Sitanion hystrix	0		0.1	0.21
Sporobolus cryptandrus	3.3	1.97	0.1	0.17
Sphaeralcea coccinea	0.1	0.18	0.1	0.24
Vulpia octoflora	4.1	2.88	4.5	3.46
Xanthocephalum sarothrae	5.1	2.80	1.1	2.16
Yucca navajoa	T		0	

tween the two sites. Conversely, sand dropseed (*Sporobolus cryptandrus*), demonstrated increased representation on the grazed sites. This may be due to the pressure of livestock foraging, reducing competition on the grazed sites by opening up the vegetation cover and thus allowing room for expansion of sand dropseed. Sand dropseed is well adapted to sandy soils and will increase or even invade if the proper conditions are present. Other species showing increases on the grazed sites were snakeweed (*Gutierrezia sarothrae*) and Russian thistle (*Salsola iberica*). Both species are considered as increasers and/or invaders on rangelands in the western United States.

Percent cover of forbs was also greater among grazed stands. Russian thistle is primarily responsible for the increased represen-

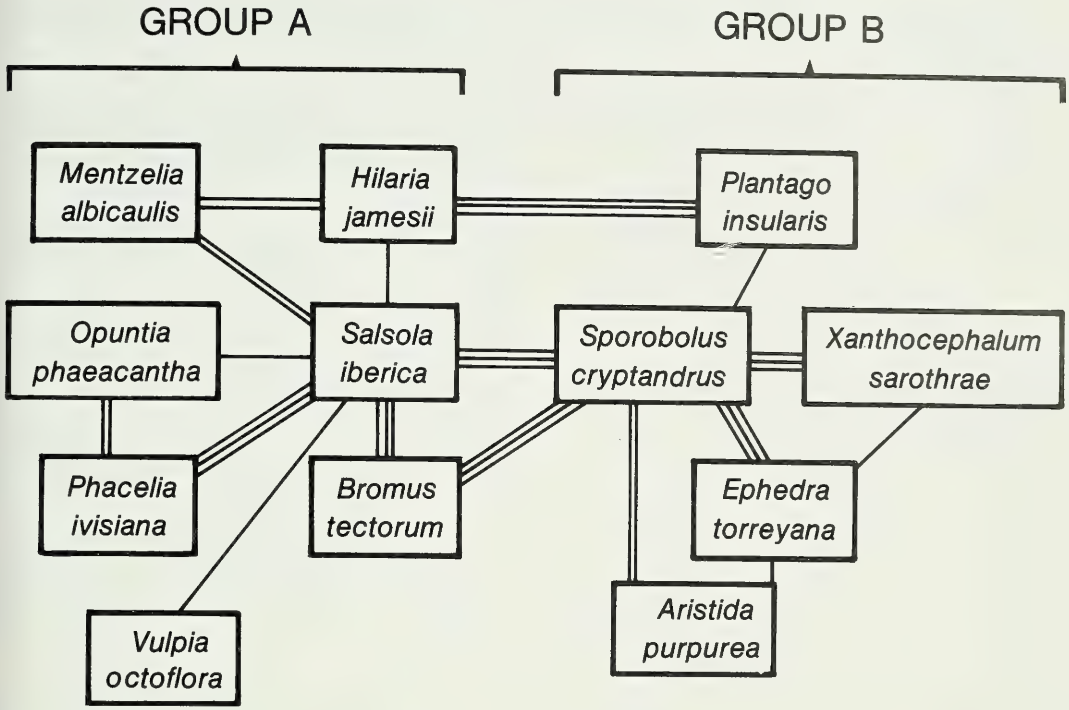
GROUP A
GROUP B
Mentzelia albicaulis
Hilaria jamesii
Plantago insularis
Opuntia phaeacantha
Salsola iberica
Sporobolus cryptandrus
Xanthocephalum sarothrae
Phacelia ivisiana
Bromus tectorum
Ephedra torreyana
Aristida purpurea
Vulpia octoflora

Fig. 4. Cluster of plant species associated with grazed and nongrazed sites as determined by Cole's (1949) Index. The more lines between the species, the greater the association. All associations are statistically significant.

tation of forbs on the grazed areas. Brotherson and Brotherson (1981) also reported greater cover of forbs in grazed sagebrush communities than in ungrazed communities. Increases in forb cover were due primarily to exotic annuals.

To further understand species interaction, niche overlap values were clustered to assess geographical association patterns among the species (Fig. 4). Five groups clustered together, three of which are of particular interest. These three groups centered around species that can be labeled decreasers, increasers, and opportunists. The remaining two groups seem of little significance. The decreasers group was characterized by winterfat and Indian ricegrass. This group also included species (winter annuals) that are not generally considered decreasers. However, all species in the group showed less cover on grazed than on ungrazed areas. The increasers include snakeweed, sand dropseed, purple threeawn (*Aristida purpurea*) and Torrey mormontea (*Ephedra torreyana*). Each of the species in this group had greater cover on the grazed sites and displayed some degree of dominance. The opportunists are generally considered unpalatable and showed increased cover on the grazed sites. This group is characterized by Russian thistle and prickly pear (*Opuntia phaeacantha*).

To define these relationships more precisely, we employed the use of Cole's (1949) Index of interspecific association (Table 4). In this case, two groups of species were apparent from the analysis. Group A contains seven species, five of which are annuals, whereas group B contains species that are mostly perennial. The species of group B are generally more important in the grazed sites with respect to cover values, and the species in group A show little preference for either side of the fence. Each group contains species that show positive affinities for species within that group and negative relationships for species found in the opposite group. The two groups

TABLE 4. Results of Cole's Index analyses with respect to the interspecific association patterns of species found growing in conjunction with winterfat populations in Kane County, Utah. Significance levels of the chi-square values are as follows: $0.05 = p \geq 3.85$, $0.01 = p \geq 6.64$, and $0.01 = p \geq 11.21$.

	Positive associations				Negative associations			
Species	Species	X^2	Coef.	SD	Species	X^2	Coef.	SD
		Group "A"						
Bromus tectorum	*Salsalo iberica*	19.5	0.286	0.064	*Ceratoides lanata*	6.0	0.299	0.122
	Sporobolus cryptandrus	11.8	0.263	0.076				
Hileria jamesii	*Mentzelia albicaulis*	10.1	0.124	0.039	*Oryzopsis hymenoides*	9.5	0.578	0.187
	Plantago insularis	13.3	0.076	0.021	*Vulpia octoflora*	6.1	0.411	0.167
	Salsola iberica	4.2	0.054	0.026				
Mentzelia albicaulus	*Salsola iberica*	6.7	0.130	0.050	*Aristida purpurea*	5.6	0.702	0.296
Opuntia phaecantha	*Phacelia iviciana*	43.2	1.000	0.152				
	Salsola iberica	4.5	1.000	0.470				
Phacelia iviciana	*Salsola iberica*	8.9	0.694	0.233	*Ceratoides lanata*	5.2	1.000	0.441
Salsola iberica	*Sporobolus cryptandrus*	11.4	0.302	0.089	*Ceratoides lanata*	14.9	0.551	0.143
	Vulpia octoflora	4.6	0.551	0.157	*Oryzopsis hymenoides*	4.4	0.185	0.088
Vulpia octoflora					*Ceratoides lanata*	5.2	0.309	0.136
					Hileria jamesii	6.1	0.412	0.167
		Group "B"						
Aristida purpurea	*Ephedra torreyana*	6.1	0.080	0.032	*Ceratoides lanata*	8.6	0.551	0.187
	Sporobolus cryptandrus	8.5	0.343	0.118	*Mentzelia albicaulis*	5.6	0.702	0.296
Ephrdra torreyana	*Sporobolus cryptandrus*	13.1	1.000	0.277	*Oryzopsis hymenoides*	13.4	1.000	0.272
	Xanthocephalum sarothrae	4.9	1.000	0.451				
Plantago insularis	*Hileria jamesii*	13.3	0.076	0.021				
	Sporobolus cryptandrus	4.1	0.224	0.112				
Sporobolus cryptandrus	*Xanthocephalum sarothrae*	28.0	0.651	0.123	*Ceratoides lanata*	19.4	0.530	0.120
Xanthocephalum sarothrae					*Ceratoides lanata*	6.8	0.201	0.077

are bridged by two species: sand dropseed and, to a lesser extent, desert plantain (*Plantago insularis*). The existence of the two groups indicates the species belonging to each group are doing quite different things with respect to their present environment. The underlying reasons for the groupings are unknown.

Also of interest from the analysis is the fact that neither winterfat nor Indian ricegrass showed any positive correlations. In both cases, all indicated relationships with other species were negative. Winterfat, for example, had a total of 16 negative correlations out of a possible total of 20. Of these, 9 were significant ($p < 0.05$). With release from grazing, the individual plants of winterfat grow to be much larger in stature and increase in density (8,409 individuals/ha in the nongrazed area vs. 2,414 individuals/ha in the grazed areas). Such changes place winterfat plants in a highly competitive position with respect to other understory species. These changes would increase winterfat's crowding and shading ability. Most of the species showing negative association patterns with winterfat are shade intolerant.

Smith (1959) indicates that patterns of interspecific association between species can change with varying degrees of grazing pressure. Further, Cook and Hurst (1962), in a study done in the Escalante deserts of southern Utah, showed that negative association patterns intensified between winterfat and the two species Indian ricegrass and yellowbrush (*Chrysothamnus stenophyllus*). The intensified negative relationships that developed with yellowbrush happened because it and winterfat responded differently to varying grazing pressures. Winterfat was shown to decrease in the face of heavy grazing pressure whereas yellowbrush increased under similar grazing conditions. The intensification of the negative associations between winterfat and Indian ricegrass developed for opposite reasons. In this case both species showed increased prominence to release from heavy grazing, but under heavy grazing conditions their association patterns were essentially neutral. This suggests the development of strong competition between the two species when they are released from grazing and growing sympatrically. Both cases appear to be happening with respect to winterfat and its interspecific association patterns as measured in our study. In the grazed areas of our study, winterfat is being eliminated as a result of winter use, and other species are expanding into the vacated space, thus creating the opportunity for increased competition and negative associations. Conversely, in the ungrazed sites winterfat is expanding in prominence, thereby creating conditions for the intensification of competition between itself and other species. Reasons are not always apparent or easily understood. To gain a total explanation, further studies of the autecology of the species involved seems necessary.

It is evident that release from winter grazing on the East Clark Bench allotment has had major impacts on the winterfat communities examined. Following 26 years without grazing pressure, floristic diversity decreased within the winterfat communities. Winterfat and Indian ricegrass showed dramatic increases in cover when released from grazing pressure. These species are likely the primary decreasers under the present management system, demonstrating lowered tolerance to grazing. It is reasonable to assume that damage to these species is due to late winter season utilization. Holmgren and Hutchings (1972) also report marked decreases in winterfat cover when the species was grazed during late winter after its growth had begun.

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ISOZYMES OF AN AUTOPOLYPLOID SHRUB, *ATRIPLEX CANESCENS* (CHENOPODIACEAE)

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ABSTRACT.— Diploid, tetraploid, and hexaploid populations of *Atriplex canescens* ($x=9$) were examined for 18 isozyme systems. Of 24 interpretable loci, only one locus (Per_1) was polymorphic. Another locus (Per_2) showed a dosage effect. Genetic distance values, D, ranged from near 0 to 0.05, which are in the normal range for local species races. Results from clonal ramets gave identical results. The data and analyses support an essentially autopolyploid origin for the polyploid populations examined.

Atriplex canescens (Pursh) Nutt. is a widely distributed shrub in western North America. It occurs in chromosome races of $2x$–$12x$. Tetraploids ($4x=2n=36$) are most common over a majority of the range of the species, but diploids and hexaploids are not infrequent in some widely distributed areas (Stutz and Sanderson 1979, McArthur and Freeman 1982). Higher polyploids are restricted in distribution. Stutz et al. (1975) presented meiotic evidence (2.18 IVs/cell, range of 0–6) indicating that the $4x$ populations are autopolyploid. Diploid ($2x$) *A. canescens* is essentially dioecious; $4x$ and $6x$ forms are trioecious—♀, ♂ and [♀, ♂] (McArthur 1977, McArthur and Freeman 1982). As might be expected in an outcrossing species, much morphological variation is evident within and between populations (McArthur et al. 1983). We undertook a study to examine isozyme patterns among polyploid levels, genders, and ecologically separated subpopulations of *A. canescens*.

MATERIALS AND METHODS

We selected four populations (Table 1) for study. One, Kingston Canyon, was divided into two subpopulations because of strikingly different ecological conditions (plant communities, slope, moisture relationships, soils—McArthur et al. unpublished data) and because Freeman et al. (1976) showed that plants of the related species *A. confertifolia* tend to segregate ♀ versus ♂ on environmentally different sites. Seven plants from each sexual state were randomly sampled from each population. Thus, we sampled 14 plants from the Little Sahara Sand Dunes, 21 from Spanish Fork Canyon, 35 from Kingston Canyon, and 21 from near Grantsville (Table 1).

Plant material for isozyme analysis consisted of actively growing leaves from rooted cuttings (McArthur et al. 1984) growing in a greenhouse. Isozyme procedures followed Leonard et al. (1981) using a vertical polyacrylamide preformed gradient gel (Pharmacia PAA 4/30)[3]. We also followed Leonard et al. (1981) for isozyme staining of all systems except for shikimate DH (Linhart et al. 1981) and NADP-MDH (Henderson 1966). Eighteen isoenzyme systems were examined (Table 2). For heterozygous loci (only peroxidase Per_1 in this study) the "dose" of each allele for polyploid plants was detected visually by observation of staining intensity of two to five replicated gels.

Standard genetic distance, D, was calculated using the formula $D = -\log_e I$, where

$$I = \frac{J_{xy}}{J_{xx}J_{yy}}$$

and J with its subscripts is the probability that alleles under consideration are identical (Hartl 1980). Allele frequency differences fo

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TABLE 1. Characteristics of sampled populations of *Atriplex canescens*.

Collection sites	Site descriptions	Chromosome numbers[a]	Sexual states
Little Sahara Sand Dunes, Juab Co., Utah	Large rolling sand dunes	2x	♀,♂
Spanish Fork Canyon, Utah Co., Utah	Steep (> 50°) canyon slope. Rocky, unconsolidated soil.	4x	♀,♂, [♀,♂]
Kingston Canyon, Piute Co., Utah	Two subpopulations: (1) alluvial fan on canyon floor; (2) steep (> 50°) talus slope.	4x	♀,♂, [♀,♂]
Near Grantsville, Tooele Co., Utah	Valley floor, sedimentary clay soils.	6x	♀,♂, [♀,♂]

[a] Little Sahara Sand Dune population and Grantsville population determined by Stutz et al. (1975 and 1979, respectively). We did counts for several plants each at Spanish Fork Canyon and Kingston Canyon following the methods of Stutz et al. (1975) and confirmed the counts for the other locations.

TABLE 2. Isozyme systems tested.

Isozyme[a]	Success	Genetics
Peroxidase	Yes	1 locus, polymorphic 1 locus, monomorphic
Glutamate DH	Yes	1 locus, monomorphic
Malate DH	Yes	1 locus, monomorphic[b]
Shikimate DH	Yes	2 loci, monomorphic
Indole Phenol Oxidase	Yes	2 loci, monomorphic
NADP - MDH	Yes	1 locus, monomorphic
LAP	Yes	2 loci, monomorphic
PGI	Yes	1 locus, monomorphic
PGM	Yes	2 loci, monomorphic
G-6-PDH	Yes	6 loci, monomorphic[a]
Amylase	Yes	2 loci, monomorphic[a]
Esterase	Yes	1 locus, monomorphic many loci, not interpretable
RBPC[c]	Yes	1 locus, monomorphic[b]
ADH	No	—
Catalase	No	—
Alkaline Phosphatase	No	—
Acid Phosphatase	No	—
GOT	No	—

[a] See Henderson 1966, Leonard et al. 1981, and Linhart et al. 1981 for full isozyme name descriptions except for RuDPC, which is Ribulose diphosphate carbohylase.

[b] Additional loci may be present but were difficult to resolve and appeared to be monomorphic.

[c] From our total protein analysis—apparently RBPC.

the Per$_1$ locus were analyzed using the Student-Newman-Keuls multiple range test following analysis of variance procedures (Woolf 1968).

RESULTS AND DISCUSSION

Of the 13 systems (24 interpretable loci) we were able to analyze, only one locus was polymorphic (Table 2). The Per$_1$ locus had slow, *s*, and fast, *f*, alleles. Under our experimental conditions (see Leonard et al. 1981) the Per$_1-s$ allele migrates about 35 mm and the Per$_1-f$ allele about 41 mm from the origin.

The isozyme data support the Stutz et al. (1975) and Stutz and Sanderson (1979) suggestion that *A. canescens* forms an autopolyploid complex. The preponderance of monomorphic loci, identical in each locus in each population, suggests genetic homogeneity inherent in autopolyploid complexes. In a similar study, Oliver and Ruiz Rejon (1980) also found identical isozymes at various polyploid levels in the apparent autoploid *Muscari atlanticum* (Liliaceae). In their study, they also found that esterase isozymes stained more intensely with increasing polyploid levels. We found an analogous situation with our Per$_2$ locus (54 mm from origin): all *A. canescens* plants had Per $_2$ monomorphically and showed a distinct dosage effect. Diploids stained lightly, tetraploids darker, and hexaploids darkest of all. Visual observation of Per$_2$ from a few plants is enough to ascertain the population ploidy level.

TABLE 3. Genetic distance, D, among the *Atriplex canescens* populations.

	Distance values				
Collection sites	1	2	3	4	5
Little Sahara Sand Dunes (1)	—				
Kingston Canyon slope (2)	.003	—			
Kingston Canyon flat (3)	.004	.000	—		
Spanish Fork Canyon (4)	.008	.000	.000	—	
Grantsville (5)	.024	.011	.011	.007	—

Ordinarily, polyploids have high levels of isozyme heterozygosity (Hamrick et al. 1979, Hunziker and Schaal 1983). That *Atriplex canescens* does not supports its probable autoploid condition. Autoploidy aside, it is another example, following Ledig and Conkle (1983), that some woody long-lived perennials have more isozymic homozygosity than previously thought, e.g., Hamrick et al. 1979. Sanderson and Stutz (1984) have recently discovered that diploids have a consistently different flavonoid pattern than do tetraploids for both *Atriplex canescens* and *A. confertifolia*. Their data can be interpreted as meaning the two ploidy levels have different flavonoid physiology.

Table 3 shows that genetic distance values among *A. canescens* populations are minimal but are in the range (D = nearly 0 to 0.05) that Nei (1976) suggested for local races of a species. All tetraploid populations had D values of nearly 0. The hexaploid population was set further from the tetraploid populations than was the diploid population. The hexaploid population may, interestingly, have some introgression from *A. tridentata* (Stutz et al. 1979), whereas the tetraploid populations appear to be strict autopolyploids. We point out that our genetic distance values reflect variation at only one of the 13 loci examined.

We examined two or more clonal ramets for isozymes from each plant and obtained identical results in each case. These results are similar to those of Sternberg (1976), who showed that separated clones of *Larrea tridentata* maintained identical isozyme patterns.

There was no statistically significant frequency difference of the Per_1 locus among the sexual phenotypes of *A. canescens* at the study sites (Table 4) even though these phenotypes differ in morphological and physiological characteristics (McArthur and Freeman 1982; McArthur et al. 1984; McArthur et al. unpublished data). However, in four of the five populations ♂'s have a higher frequency of the Per_1-s allele than do ♀'s. The change in frequency of the Per_1-s allele from diploid to tetraploid to hexaploid is interesting and warrants further attention.

Interesting, too, is that *A. canescens* is dioecious or trioecious. These sexual systems have long been considered to have evolved due to inbreeding depression (Grant 1975, Lloyd 1982). Given the monomorphic isozyme data for loci that are normally highly polymorphic (Table 2), it is difficult to see how inbreeding depression, in this case, could be as potent as is required to create the dioecious state. Krohne et al. (1980) discounted inbreeding depression as the driving force in the gynodioecious breeding system of *Plantago lanceolata*.

ACKNOWLEDGMENTS

The study was facilitated by National Science Foundation Grant DEB 81-11010 and Pittman Robertson Wildlife Restoration Project W-82-R. We thank Drs. F. T. Ledig, Y. B. Linhart, J. B. Mitton, and H. C. Stutz for constructive criticism of earlier versions of this manuscript.

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TABLE 4. Frequency of the Per$_1-s$ allele.

Population	Frequency			
	Mean ± se	♀	♂	[♀,♂]
Little Sahara Sand Dunes (2*x*)	.921 ± .057A[a]	.850	1.00	—
Kingston Canyon slope (4*x*)	.647 ± .071B	.643	.667	.625
Kingston Canyon flat (4*x*)	.643 ± .081B	.625	.667	—[b]
Spanish Fork Canyon (4*x*)	.583 ± .052B	.536	.643	.571
Grantsville (6*x*)	.258 ± .040C	.286	.238	.250

[a] Different letters after mean frequency values indicate significantly different ($p < .01$) means.

[b] [♀, ♂] ramets from Kingston Canyon flat were not available for study at the same time as the other populations; consequently they were not included.

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WINTER NUTRITIVE CONTENT OF BLACK SAGEBRUSH (*ARTEMISIA NOVA*) GROWN IN A UNIFORM GARDEN[1]

Barbara Behan[2] and Bruce L. Welch[3]

ABSTRACT.— Winter crude protein content, in vitro digestibility, and productivity were determined for seven accessions of black sagebrush (*Artemisia nova*) grown in a uniform garden. No significant differences were detected among the accessions for any of these attributes. Mean crude protein was 6.8% of dry matter. Accessional range was from 5.8% to 7.3%. Mean in vitro digestion was 54.8% of dry matter; accessional range, 51.9% to 57.2%. Mean current year's growth (a measurement of productivity) was 4.3 cm; accessional range, from 3.7 to 5.1 cm. In comparison to other winter forages, black sagebrush ranks high for winter levels of crude protein and very high in winter digestible dry matter but low in productivity.

Protein and energy-producing compounds are two of three nutrients commonly listed as being deficient in the winter diet of ruminants on native ranges (Dietz 1965, Halls 1970, Nagy and Wallmo 1971, Welch and McArthur 1979a). Plants that retain significant amounts of green leaves during the winter usually contain higher levels of protein and are more digestible than those that shed their leaves (Ensminger and Olentine 1978, Welch 1983). We have reported significant differential preference of wintering mule deer (*Odocoileus hemionus hemionus*) among seven accessions of black sagebrush (*Artemisia nova*) (Behan and Welch 1985). Significant variation in winter nutrient levels among accessions of a related species, big sagebrush (*A. tridentata*), grown in a uniform garden has been reported (McArthur and Welch 1982, Welch and McArthur 1979b, Welch and Pederson 1981), but there has been little information until now concerning variation in winter nutrient levels among accessions of black sagebrush. We undertook this study to determine the winter nutritive content of seven accessions of black sagebrush grown in a uniform garden.

MATERIALS AND METHODS

On a uniform shrub garden located at the Gordon Creek Wildlife Management Area[4] near Helper, Utah, seven accessions were selected to determine in vitro digestibility, productivity, and levels of crude protein. The accessions had been transplanted as seedlings from various native source locations (Table 1). Within each accession, seven individual plants were randomly selected to furnish the vegetative tissue needed for testing. Because of heavy grazing on twig tips by wintering mule deer, composite sampling had to be used for the Spring Valley and Wingate Mesa accessions. Only twigs with terminal buds and leaves were collected from the plants. Sampling occurred on 3 December 1982.

Vegetative samples (current year's growth of stems and leaves) were collected from each plant, placed in separate paper bags and frozen on site with dry ice. Individual samples were placed in separate plastic bags tied and sealed in a second bag. The double-bagged samples were stored at −35 C until ground.

The samples were ground while submerged in liquid nitrogen in a motorized mortar and pestle. This was done to prevent loss of volatile substances such as monoterpenoids that may suppress cellulolytic microorganisms and to aid in grinding the samples (1/2 mm, Hobbs et al. 1985). Next the ground samples were stored in airtight containers at −35 C until needed for protein determination or digestion trials.

Crude protein levels were determined by the Kjeldahl method (Association of Official

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[1] This article was written by a United States government employee and a federal cooperator on official time and is therefore in the public domain.

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[4] The shrub garden at the Gordon Creek Wildlife Management Area is cooperatively maintained by the Utah Division of Wildlife Resources (Wildlife Restoration funds W-82-R, job 1) and the Intermountain Research Station.

TABLE 1. Locations by county, state, and landmark, or town where each of seven accessions of black sagebrush (*Artemisia nova*) were collected.

Accession	Location
Pine Valley Ridge	Millard, Utah (Desert Experimental Range)
Manti	Sanpete, Utah (Manti)
Black Mountain	Sevier, Utah (Salina)
Spring Valley	White Pine, Nev. (Jct. US-93, 6, and 50)
Dove Creek	Dolores, Colo. (Dove Creek)
Wingate Mesa	San Juan County, Utah (Fry Canyon)
Fremont Junction	Sevier, Utah (Fremont Jct.)

TABLE 2. Mean winter crude protein, in vitro digestibility, and productivity for seven accessions of black sagebrush (*Artemisia nova*) grown in a uniform garden. Protein and digestibility data are expressed as percent of dry matter. Productivity data are expressed in length of leader growth in centimeters. Means for all measurements were found not to be significantly different.

Accession	Crude protein (%)	Digestibility (%)	Leader growth (cm)
Spring Valley[1]	5.8	54.6	3.7
Manti	6.5	57.2	4.1
Black Mountain	6.9	55.9	3.7
Fremont Junction	6.9	55.6	5.1
Dove Creek	7.1	55.6	4.6
Wingate Mesa[1]	7.2	51.9	3.9
Pine Valley Ridge	7.3	53.5	4.5

[1] Samples of the Spring Valley and Wingate Mesa accessions were composited and not included in the analysis of variance.

Analytical Chemists 1980). Crude protein data are expressed as a percentage of dry matter. We used the in vitro digestion procedure as outlined by Pearson (1970), except 1.0 g of fresh tissue was placed in digestion tubes. Rumen inoculum was collected from a slaughterhouse steer fed a ration of alfalfa hay and corn. Welch et al. (1983) have reported that inoculum source has little effect on the ranking of the digestibility of range forages. Results of the digestion trials are expressed as a percentage of dry matter digested.

Percentage values for the crude protein were transformed (arcsin) before performing a completely random analysis of variance. Percentages for in vitro digestion were in the range that did not require transformation prior to the analysis of variance. For significant F ratios, Student-Newman multiple range test ($P < 0.05$) was used to determine differences among treatment means. Because of the composite sampling, the Spring Valley and Wingate Mesa accessions were not included in the analysis of variance for crude protein and in vitro digestion.

Prior to deer use, the plants were used to determine current year's growth, an indicator of production. Current year's growth was determined by measuring the annual leader length of 15 leaders per plant. Leader lengths were measured to the nearest centimeter from the terminal leaf bud scars to the tip of the current terminal leaves. The leaders were selected at random over the entire crown of the plants. A plant mean was calculated from the 15 measurements. Current year growth data were expressed as centimeters and were statistically analyzed as described for crude protein and in vitro digestion.

RESULTS AND DISCUSSION

Results of the crude protein determinations are given in Table 2. Mean winter crude protein content for black sagebrush was 6.8%. Accessional range was from 5.8% to 7.3%. The Pine Valley Ridge accession contained the highest amount of crude protein at 7.3%. No significant differences among the accessions were detected.

Our crude protein levels are considerably less than the 11.7% level reported by Sheehy (1975) and less than the 8.5% reported by the National Academy of Sciences (1964). We are not sure that the latter figure was for the winter period. Averaging the three studies, black sagebrush winter crude protein content would be about 9.0% of dry matter. A winter crude protein level of 9.0% ranks high among winter range forages (Table 3).

Winter in vitro digestibility of the seven accessions of black sagebrush is given in Table 3. Mean in vitro digestibility was 54.8% of dry matter digested. Accessional range was from 51.9% to 57.2%. The Manti accession was the most readily digested at 57.2%. No significant differences were detected among the acces

TABLE 3. Mean winter crude protein content (percentage of dry matter) of some range plants.

Plant	Crude protein	Range	Reference
Agropyron desertorum (green-regrowth)	15.0		19*
Artemisia tridentata	11.4	(9.9–14.2)	1, 2, 3, 4, 6, 8, 12, 16, 19
Cercocarpus ledifolius	10.1	(9.6–10.6)	3, 7
Atriplex canescens	9.6		11
Artemisia nova	9.0	(6.9–11.7)	12, 20, 17
Prunus virginiana	8.7	(7.6–9.9)	3, 5, 10, 15
Cowania mexicana	8.6	(8.4–8.8)	5, 13
Purshia glandulosa	8.5	(8.0–9.0)	3, 13
Juniperus scopulorum	8.4		1
Populus tremuloides	7.8	(6.5–9.5)	3, 10, 15
Chrysothamnus nauseous	7.8	(5.9–7.8)	1, 10
Cercocarpus montanus	7.8	(7.2–8.4)	1, 5, 8
Purshia tridentata	7.8	(6.7–9.1)	1, 3, 4, 7, 8, 10, 13
Atriplex confertifolia	7.7		9
Juniperus osteosperma	6.6	(5.9–7.6)	3, 5, 7
Chrysothamnus viscidiflorus	5.9		19
Amelanchier alnifolia	5.9	(5.5–6.2)	3, 10
Rosa woodsii	5.8	(5.4–6.1)	15, 18
Quercus gambelii	5.3	(5.1–5.4)	5, 16
Fallugia paradoxa	4.8		13
Amelanchier utahensis	4.8		15
Agropyron desertorum	3.9		10
Native grass	3.6		3
Stipa comata	3.5	(2.9–4.0)	9, 10
Oryzopsis hymenoides	3.0	(2.5–3.5)	10, 17

*Reference:
1. Dietz et al. 1962
2. Welch and McArthur 1979b
3. Tueller 1979
4. Bissell et al. 1955
5. Smith 1957
6. Smith 1950
7. Smith 1952
8. Medin and Anderson 1979 (Data converted to dry matter basis)
9. National Academy of Sciences 1975
10. National Academy of Sciences 1958
11. Welch and Monsen 1981
12. Sheehy 1975
13. Welch et al. 1983a
14. Welch and Monsen 1984
15. Dietz 1972
16. Kufeld et al. 1981
17. National Academy of Sciences 1964
18. Welch and Andrus 1977
19. Urness et al. 1983
20. This study

sions. Our mean in vitro digestibility compares favorably with reports by Sheehy (1975) at 53.1% and with Welch et al. (1983b), also at 53.1%. Mean in vitro dry matter digestibility for the three studies is 53.7%. Black sagebrush ranks very high in digestibility among winter range forages (Table 4). Ammann et al. (1973) estimated that dry-matter digestibility of 50% would provide sufficient energy for maintenance.

Mean current year's growth was 4.3 cm, accessional range, 3.7 to 5.1 cm. The Fremont Junction was the most productive at 5.1 cm (Table 2). No significant differences among the accessions were detected. Black sagebrush is not as productive as other winter range forages such as big sagebrush (*Artemisia tridentata*), antelope bitterbrush (*Purshia tridentata*), fourwing saltbush (*Atriplex canescens*), and true mountain mahogany (*Cercocarpus montanus*) (McArthur and Welch 1982, McArthur et al. 1983). Black sagebrush is adaptable to sites where the more productive species do not grow.

Black sagebrush ranks high in winter levels of crude protein and very high in digestible dry matter in comparison to other forages. Phosphorus content is probably high also (National Academy of Sciences 1964). From a qualitative point of view winter nutrient content of black sagebrush is exceeded only by big sagebrush (Tables 3 and 4; Welch 1983).

Lack of significant differences among the seven accessions for the three characters tested suggests that breeding and selection schemes stressing improvement of these attributes would be fruitless. We have reported earlier that wintering mule deer significantly preferred the Pine Valley Ridge accessions over the other accessions tested (Behan and

TABLE 4. Mean winter in vitro digestion of some range plants. Data are expressed as a percentage of dry matter digested.

Plant	Dry matter digested	Range	Reference
Artemisia tridentata	57.4	(49.9–67.0)	2, 3, 4, 5, 6, 7, 10*
Artemisia spinescens	57.0		8
Artemisia nova	53.7	(53.1–54.0)	3, 8, 14
Sporobolus cryptandrus	53.2		8
Agropyron smithii	50.2		10
Oryzopsis hymenoides	50.0	(45.7–54.2)	8, 10
Cercocarpus ledifolius	49.1	(44.7–53.5)	4, 6
Rosa eglanteria (hips)	49.1		6
Hilaria jamesii	48.2		8
Stipa comata	48.1		10
Agropyron spicatum	45.5		10
Ceratoides lanata	44.7		8
Chrysothamnus nauseous	44.4		10
Atriplex confertifolia	43.4		8
Amelanchier utahensis	41.0		1
Prunus virginiana	38.8	(26.3–51.3)	1, 11
Atriplex canescens	38.3		9
Cowania mexicana	37.6		12
Purshia glandulosa	35.8		12
Amelanchier alnifolia	34.6		10
Kochia prostrata	32.2		13
Fallugia paradoxa	29.8		12
Quercus gambelii	28.1		2
Purshia tridentata	25.4	(19.8–30.0)	4, 6, 10, 12
Cercocarpus montanus	24.3	(20.0–28.5)	4, 6

*References:

1. Dietz 1972
2. Kufeld et al. 1981
3. Sheehy 1975
4. Urness et al. 1977
5. Wallmo et al. 1977
6. Welch and Pederson 1981
7. Pederson and Welch 1982
8. Welch et al. 1983b
9. Welch and Monsen 1984
10. Ward 1971
11. Uresk et al. 1975
12. Welch et al. 1983a
13. Welch and Davis 1984
14. This study

Welch 1985). Also, Clary and Beale (1983) noted that pronghorn and domestic sheep both preferred black sagebrush that grows on the Desert Experimental Range in Pine Valley. This is the same kind of black sagebrush as our collection from the Pine Valley Ridge (just north of the Desert Experimental Range). We will be testing the adaptation range of the Pine Valley Ridge accession in preparation for releasing it through the Soil Conservation Service's plant material program as a superior cultivar of black sagebrush for improving winter ranges for domestic sheep, pronghorn, and mule deer.

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WINTER FOOD HABITS OF THE PINE MARTEN IN COLORADO

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ABSTRACT.—Eighteen pine marten (*Martes americana*) stomachs and 29 intestinal tracts, collected between October 1983 and March 1984 from northern Colorado, were examined for food items. Voles (*Microtus* spp.) occurred most frequently, followed by shrews (*Sorex* spp.), insects, and vegetative matter.

The pine marten (*Martes americana*) inhabits mature stands of coniferous forests of North America (Lensink et al. 1955, Marshall 1951). Although the pine marten is an important furbearer in many states, few studies have specifically examined winter food habits (Hargis and McCullough 1984, Zielinski et al. 1983, Lensink et al. 1955, Cowan and Mackay 1950). Winter is a critical period when many food items are unavailable and prey populations reach yearly lows. Lensink et al. (1955) reported that changes in the abundance or availability of food may be reflected in movements, productivity, and choice of habitat. The objectives of this study were to identify winter foods and their frequencies in the diet with respect to availability.

STUDY AREA AND METHODS

The study area is in the Roosevelt National Forest 29 km west of Rustic, Larimer County, Colorado. Elevation ranged from 3168 to 3780 m. The trap sites were dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). The main understory vegetation consisted of vaccinium (*Vaccinium* spp.). The study was conducted from October 1983 to March 1984. The winter was severe with greater snowfall and colder temperatures than average.

Thirty-two martens were collected using conibear and leghold traps. Food samples were taken from both the stomach and intestine. Samples were analyzed using the procedure described by Johnson and Hanson (1977). Reference collections were used to identify diagnostic bones, teeth, hair, or feathers. Hair impressions were used when no other fragments were identifiable (Moore et al. 1974). Prey items were identified to genus whenever possible. Percent occurrence (number of occurrences of a prey item/total number of stomachs or intestines ×100) was determined for each prey item.

RESULTS

Twelve different food items were identified in stomach and intestinal samples (Table 1). Mammals composed the highest percentage of items found. *Microtus* spp. were the most important food item, occurring in 83% of the samples. Although insects and vegetative materials were represented in 17% of the samples, actual amounts per scat were negligible. Birds, squirrels (*Tamiasciurus hudsonicus*), cervids, and fish were present in 11% of the diets. Mustelids constituted 10%; however this is believed to have been ingested incidentally. Both snowshoe hare (*Lepus americana*) and beaver (*Castor canadensis*) items occurred in 7%.

DISCUSSION

Microtus spp. were also the most important food item in previous studies (Douglass et al. 1983, Zielinski et al. 1983, Soutiere 1979, Weckwerth and Hawley 1962, Murie 1961, Quick 1955, Lensink et al. 1955, Cowan and Mackay 1950). The results of small mammal trapping have shown microtines to be the most abundant small mammals in the area during winter (Palmer, progress report). Although shrews were quite abundant on the

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TABLE 1. Stomach and intestinal contents from 32 Colorado pine marten, October 1983–March 1984.

	Percent occurrence in stomach (N=18)	Percent occurrence in intestine (N=29)
Mammals		
Microtus spp.[a]	83	79
Sorex spp.[b]	39	45
Tamiasciurus hudsonicus	11	7
Lepus americana	5	7
Castor canadensis	5	5
Cervidae	11	3
Mustelidae	5	10
Birds[c]	11	7
Fish	11	3
Vegetation	11	17
Insects	17	14
Unknown	0	3

[a] Includes *M. pennsylvanicus, M. longicaudus, M. montanus, Clethrionomys gapperi, Phenacomys intermedius.*

[b] Includes *S. hoyi, S. vagrans, S. cinereus, S. palustris, Cryptotis parva.*

[c] Includes *Turdis migratorius, Junco hyemalis caniceps,* and two samples keyed only to Passeriformes.

study site, the high prevalence in marten diets was unusual (Palmer, progress report). Generally shrews are not taken, although they may be quite abundant, because they have musk glands that emit a strong odor (Lensink et al. 1955, Cowan and Mackay 1950). The high percentage of shrews may be directly related to the severity of the winter and prey abundance. Colder winters and deeper snows reduce aboveground activity of mammals (Ewer 1973), and the marten minimizes activity by taking the most abundant food source. *Sorex* spp. were the second most abundant food source available during winter. Birds occurred infrequently, suggesting that they were taken only when chance permitted. Similar results were reported by Weckwerth and Hawley (1962), Lensink et al. (1955), and Cowan and Mackay (1950). A relatively low percentage of the samples contained pine squirrel. Although no index of abundance was available for comparison, pine squirrels are believed to exhibit periods of torpor during winter and are virtually unavailable to the marten (Cowan and Mackay 1950). The cervid noted was most likely carrion. The fish and beaver were probably obtained from other trappers' bait or discarded portions of carcasses left in the area. Snowshoe hares, though occurring on the study area, were seldom taken by martens. Other studies have reported similar results (Douglass et al. 1983, Lensink et al. 1955, Cowan and Mackay 1950).

Marten food habits are affected by availability, preference, and availability of alternate prey (Weckwerth and Hawley 1962). Zielinski et al. (1983) reported that seasonal activity of the marten appeared to be synchronized with the activity of its prey. Marten activity varies seasonally. They are crepuscular during the summer, but the approach of winter forces them to become nocturnal as alternate food sources become less available (Zielinski et al. 1983). The availability of invertebrates, fruits, birds, and diurnal mammals increases during warm spring and summer months. During winter, insects decrease in abundance, migrant bird populations have gone, and fruit no longer remains on bushes (Weckwerth and Hawley 1962). Colder temperatures and deep snows force many mammals underground; therefore, few prey items are still available to the martens. Nocturnal activity increases the martens' interactions with prey species such as voles, shrews, or snowshoe hares. It is therefore not surprising that voles and shrews were taken most frequently. It appears that food items on the study area were taken in proportion to their abundance and availability. This study, like others, shows that martens at this particular study area are opportunistic in nature during critical periods in order to optimize net energy gained (Quick 1955, Lensink et al. 1955, Weckwerth and Hawley 1962).

ACKNOWLEDGMENTS

I express my gratitude to M. W. Schehrer and G. E. Graves for their help and encouragement. I also thank Terry Foppe and the Colorado State University Composition Laboratory for use of facilities and Charles Chase III, curator of ornithology, Denver Museum of Natural History.

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FOLIAGE AGE AS A FACTOR IN FOOD UTILIZATION BY THE WESTERN SPRUCE BUDWORM, *CHORISTONEURA OCCIDENTALIS*

Elizabeth A. Blake[1] and Michael R. Wagner[1]

Abstract.—The influence of current year foliage age on food consumption and utilization by the western spruce budworm, *Choristoneura occidentalis* (Lepidoptera:Tortricidae). was examined. Larvae were fed immature foliage of **Douglas-fir (*Pseudotsuga menziesii*** var. *glauca*), Engelmann spruce (*Picea engelmannii*), and corkbark fir (*Abies* ***lasiocarpa*** **var. *arizonica*) in June** and August of 1981 and Douglas fir in June and July of 1982. All larvae feeding on **early season (June) foliage** reached maturity. Larvae feeding on middle (July) and late (August) season foliage died **before reaching pupation. Relative growth rate** and efficiency of conversion of ingested food decreased with foliage age **in both the 1981 and 1982 experiments.** Relative consumption rate increased with foliage age in the 1981 and decreased **in the 1982 experiment.**

The normal free-feeding period for western spruce budworm, *Choristoneura occidentalis* Freeman, larvae begins in early spring at host bud burst. The larvae feed primarily on immature host foliage, ingesting mature foliage only when the preferred diet is unavailable. Nutrient content and ease of ingestion and digestibility are often greater in immature foliage than in mature foliage (Heron 1964, Scriber and Slansky 1981). Host defenses such as lignins, silica, tannins, oils, waxes, and resins often increase with foliage age. Such changes in food quality may be responsible for the western spruce budworm's preference for early season foliage.

The purpose of this study was to determine the influence of the age of current year foliage on consumption and utilization by the western spruce budworm.

Methods

Feeding experiments were conducted 13 June-4 July and 10 August-25 August in 1981 and again 16 June-10 July and 10 July-30 July in 1982. Larvae were collected from the field and reared individually in 150 × 25 mm petri dishes at 16L:8D and 24–26 C during the feeding experiments. Sixteen replicates were set up for each year and season. Host tree and larvae selection and calculation of nutritional indices followed Wagner and Blake (1983). Collection of larvae and foliage, preparation of foliage for feeding, and calculation of ingested foliage differed in 1981 and 1982.

To standardize the host phenological stage, early season feeding experiments were begun when the foliage was at the "brush" stage (bud cap gone, needles flaring but no shoot growth so needles appear to arise from one location) (Shepherd 1983). The middle season feeding experiment conducted in 1982 was begun after all the larvae used in the early season experiment had pupated. The 1981 late season feeding experiment was conducted in early August, after the natural insect population had ceased feeding in the field.

1981 Feeding Experiment

When *C. occidentalis* larvae were collected in the field, no attempt was made to segregate them based on the host foliage from which they were collected. Third instar larvae were selected for the first seasonal experiment using head capsule measurements (Bean and Batzer 1957, Wagg 1958). The remaining larvae were reared to pupation, mated, and allowed to oviposit. When the eggs hatched, the larvae were placed on artificial diet to feed. Those larvae that did not diapause were selected from the population and reared to the fourth instar on artificial diet. Larvae were moved to natural foliage 48 hours before the second seasonal experiment was begun. A minimum of 24 hours was necessary for successful acceptance and assimilation of a food source by the budworm larvae (Jacqueline Lee Robinson, personal communication).

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Foliage was collected at random from the lower crown of Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco, corkbark fir, *Abies lasiocarpa* var. *arizonica* (Merriam) Lemm., and Engelmann spruce, *Picea engelmannii* Parry ex. Engelm. trees located approximately 16 km north of Flagstaff, Arizona. Previous years' needles were clipped from the stem, and the twigs, with only current year foliage attached, were weighed.

The foliage twigs were replaced every 72 hours, and the twigs that had been fed upon were oven dried (60 C until no further weight loss occurred) and weighed. Foliage ingested was calculated on a dry weight basis as follows:

$$W_I=(W_F \cdot X)_B-DW_A$$

where:

W_I=dry weight of foliage ingested (mg)

W_F=fresh weight of the foliage twig before feeding (mg)

X=% dry weight of an aliquot foliage twig

DW_A=dry weight of the foliage twig after feeding (mg)

The aliquot twig used to calculate the initial dry weight of each feeding twig was selected for uniformity in size and phenological stage from the same host tree that provided the feeding twig.

Each replicate was terminated at pupation or when the larvae stopped feeding. Pupae and total feces for each replicate were oven dried and then weighed. Total foliage ingested was calculated and duration was noted for each replicate. Data were analyzed using a one-way analysis of variance (AOV) with alpha equal to 0.10.

1982 Feeding Experiment

Third instar larvae were collected from Douglas-fir trees in the Kaibab National Forest, North Kaibab Ranger District, Arizona. Larvae used for the early season experiment were allowed to feed on Douglas-fir foliage and advance to the fourth instar. Larvae used for the middle season feeding experiments were placed in cold storage at the time of collection to retard their development. These larvae were brought to room temperature five days before the experiment was to begin and allowed to advance to the fourth instar.

Foliage used for the 1982 feeding experiment was collected from a single medium vigor (Waring et al. 1980) Douglas-fir tree. Paired foliage samples, selected for uniformity in size and phenology, were collected from midcrown at the four cardinal directions. One twig was used to determine the average dry weight per needle; the other foliage twig was used to feed one budworm larva. The average weight per needle was later used to estimate the dry weight of the foliage consumed by the insect. Foliage was replaced every 72 hours to assure freshness and acceptability.

Each replicate was terminated at pupation or when feeding ceased. Total foliage ingested was calculated; pupae and feces were oven dried and then weighed. After calculating the nutritional indices, data were analyzed using a one-way AOV, with alpha equal to 0.10.

RESULTS AND DISCUSSION

Total foliage ingested was eliminated from the data analysis because the length of feeding time was highly variable between the feeding seasons. Nutritional indices for early, or normal, season feeding were calculated for larvae that had pupated. All the larvae feeding on middle (1982) and late (1981) season foliage died before reaching pupation. However, the nutritional indices were still calculated for larvae that fed for at least 10 days. The percent o larvae that survived until pupation was calculated for each experiment.

Results of the 1981 experiment using Douglas-fir foliage showed significant difference between early and late season foliage for al the nutritional indices calculated (Table 1). Budworms feeding on late season foliage appear to have increased their relative consumption rate (RCR) to compensate for a decrease in efficiency of conversion of ingeste food to body weight (ECI). Despite this effort *C. occidentalis* larvae were unable to maintai a relative growth rate (RGR) statistically equa to budworms feeding on early season foliage.

Larvae feeding on Engelmann spruce foliage followed the same pattern of food utilization as larvae feeding on Douglas-fir foliag

TABLE 1. Effect of Douglas-fir foliage age on food utilization by western spruce budworm (1981).

		Food utilization indices		
Season	Survival %	Relative consumption rate	Relative growth rate	ECI
Early (16,4)[b]	25	3.00 A[a]	0.09 A	5.08 A
Late (16,4)	0	9.28 B	0.01 B	0.16 B
F-Prob.		0.07	0.02	0.02

[a] One-way AOV, $\alpha = 0.10$, values followed by different letters are significantly different.
[b] Numbers in parentheses are, respectively, initial number of larvae and number of larvae used to calculate nutritional indices.
ECI = Efficiency of ingested food to body weight.
Designations apply for three following tables.

TABLE 2. Effect of Engelmann spruce foliage age on food utilization by western spruce budworm (1981).

		Food utilization indices		
Season	Survival %	Relative consumption rate	Relative growth rate	ECI
Early (16,3)	19	1.33 A	0.15 A	11.65 A
Late (16,2)	0	4.19 B	−0.05 B	−1.34 B
F-Prob.		0.01	0.01	0.01

TABLE 3. Effect of corkbark fir foliage age on food utilization by western spruce budworm (1981).

		Food utilization indices		
Season	Survival %	Relative consumption rate	Relative growth rate	ECI
Early (16,2)	13	2.67 A	0.13 A	4.78 A
Late (16,5)	0	4.70 A	0.06 A	3.24 A
F-Prob.		0.50	0.24	0.56

TABLE 4. Influence of Douglas-fir foliage age on food utilization by western spruce budworm larvae (1982).

		Food utilization indices		
Season	Survival %	Relative consumption rate	Relative growth rate	ECI
Early (16,6)	38	1.58 A	0.08 A	5.08 A
Middle (16,2)	0	1.05 B	−0.08 B	−8.02 B
F-Prob.		0.02	0.0002	0.0014

(Table 2). Although their average RCR increased significantly, the mean larval weight was significantly lower in the late season experiment when compared to the mean weight of larvae reared on early season foliage. In fact, the larvae that were fed late season foliage lost weight, probably as a result of a negative average ECI.

No significant differences were found between seasons for the three indices reported when *C. occidentalis* larvae were fed corkbark fir foliage (Table 3). However, the pattern of change in food utilization was similar to the results of the experiments using Douglas-fir and Engelmann spruce.

Significant differences were found in utilization between early and middle season feeding in 1982 (Table 4). RGR and ECI decreased significantly, which follows the pattern of the 1981 experiment. However, RCR also decreased significantly during the middle season feeding rather than increasing as predicted by Waldbauer (1968) and the 1981 feeding experiments. The larvae may have encountered chemical or physical feeding deterrents in the middle season foliage that resulted in low RCR. This result could also have been due to the period of cold storage used to slow larval development, which may have been retarded to the point where the larvae could not recover.

The statistical results of the foliage age experiments conducted in 1981 and 1982 can only be compared as to their relative patterns. Actual numbers should be disregarded due to the inconsistency in initial larval stage.

CONCLUSIONS

Host foliage phenology appears to greatly influence the food utilization and developmental success of *C. occidentalis*. Although no chemical tests were conducted on the foliage used for these experiments, the significant changes in RCR, RGR, and ECI suggest that chemical and physical changes may be occurring during the growing season. As predicted by Waldbauer (1968) and Scriber and Slansky (1981), RCR was significantly greater and ECI was significantly lower for budworms feeding on late season foliage than for those feeding on early season foliage in 1981. Despite this apparent effort to compensate for a suboptimal food source, the budworm larvae feeding on late season foliage were unable to complete their development.

The overall pattern of decreased RGR and ECI and the survival rate of the larvae feeding on middle season foliage in 1982 are comparable to those of the 1981 experiments. The decrease in RCR from the early to the middle season experiment does not follow the 1981 pattern. This may be due to chemical or physical feeding deterrents that could not be overcome by the budworm larvae.

Budworm larvae feeding on middle and late season foliage experience retarded development and mortality, though many feed as long as successful larvae that feed on early season foliage. These findings are consistent with those of Heron (1964), who studied *C. occidentalis* feeding on mature white spruce needles.

The feeding behavior of *C. occidentalis* appears to be adapted for making the most of the nutrients provided by the foliage of its host early in the growing season, while avoiding the physical and chemical defenses that may increase as the foliage matures. Studies of the physical and chemical changes in the foliage of these host trees as the growing season progresses are needed to better understand the feeding behavior of the western spruce budworm.

ACKNOWLEDGMENT

Work leading to this publication was funded in whole or in part by a program sponsored by the USDA Forest Service entitled Canada/United States Spruce Budworm Program–Science and Education Administration Agreement 59-2042-1-3-013-0.

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APPLE MAGGOT (*RHAGOLETIS POMONELLA*) ADAPTATION FOR CHERRIES IN UTAH

Clive D. Jorgensen[1], Darin B. Allred[1], and Richard L. Westcott[2]

ABSTRACT.—The apple maggot, *Rhagoletis pomonella* (Walsh) is reported from Utah County, Utah, where it has adapted to sour cherries. It has been taken repeatedly from pheromone traps in the vicinity of hawthorn (*Crataegus douglassii*), but there are no Utah data that suggest it has adapted to apples.

The apple maggot, *Rhagoletis pomonella* (Walsh), was first collected in Utah in 1976 from a Malaise trap in the Willard Basin of Box Elder County, Utah. This site was close to hawthorn, but 5 mi from the nearest apple trees. The apple maggot was not reported from Utah again until 1983 when the Utah Department of Agriculture (Edward J. Bianco, personal communication) took numerous specimens in the Mapleton (Utah County) area while trapping cherries for the western cherry fruitfly (*Rhagoletis indifferens* Curran). Trapping for apple maggots was intensified on cherries and apples in 1984.

Continuous trapping (Pherecon® AM traps) in an unsprayed cherry orchard (1984) resulted in an emergence curve that seemed optimally synchronized with sour cherries (Fig. 1). Emergence was somewhat late for sweet cherries, unless they were left on the trees or were late varieties (e.g., Lambert). Perhaps the most interesting observation was the general paucity of adults collected when most commercial apples in Utah were ripening. There was a slight increase in the number of trapped specimens in late September that may have resulted from a partial second generation, but this has not been confirmed. Early apples would be expected to ripen dur-ing the latter part of this emergence curve (Fig. 1).

The apple maggot has apparently become adapted to cherries in the Mapleton, Utah, area. Although it is tempting to suggest genetic adaptation has occurred in the population, it is more likely the adaptation to cherries is a phenological phenomenon within the population. Phenological adaptation of this type by apple maggots is certainly not new. It has been reported by Illingworth (1912), Pickett and Neary (1940), Bush (1969), Reissig and Smith (1978), Diehl (1983), and others. Bush (1974), Reissig and Smith (1978), Prokopy et al. (1982), and Diehl (1983) suggested this allochronic isolation was important in evolution of the two sympatric host races in eastern North America, one for apples and the other for hawthorn (*Crataegus* spp.).

Although we have found synchrony in apple maggot emergence with sour cherry development in Utah, it is not yet clear if an alternative host is present that provided the original source of apple maggots. Our work in 1985 has demonstrated a possible alternate host (hawthorn, *Crataegus douglassii*) that could provide this niche (Allred, unpublished data). It seems reasonable to suppose that allochronic isolation could develop in two directions from hawthorn in Utah:

Sour Cherry (early emergence) ———— Hawthorn

Hawthorn ———— Apple (late emergence)

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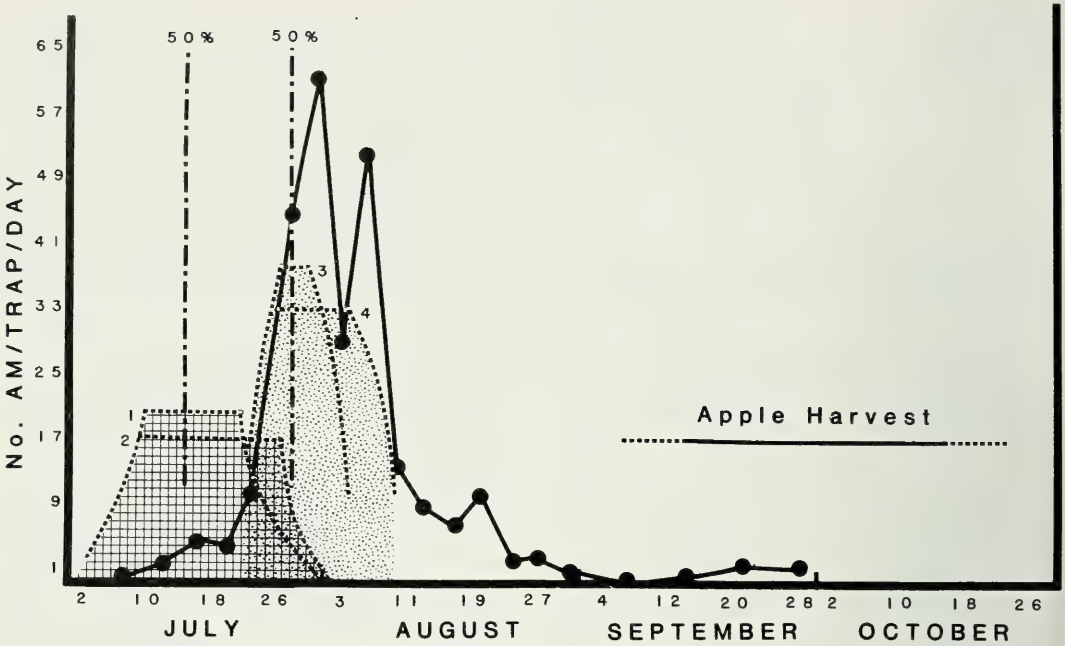

Fig. 1. Emergence curve for apple maggot (*Rhagoletis pomonella*) and its synchrony with sweet (cross-hatch) and sour (stipple) cherry harvest in central Utah, 1984. A 50% harvest for each is indicated.

This possible phenomenon seems even more plausible when one considers the fact that almost all Utah apples are the late, hard varieties—Golden Delicious, Red Delicious, and Roman Beauty. The economic implications of a possible synchronization with sour cherries, hawthorn, and apples are substantial.

Such an extended synchronization to include three fruits by the apple maggot in Utah seems rather unlikely, if data reported in eastern North America are transferrable to our population. Bush (1969) and Reissig and Smith (1978) reported that apple host races emerged several weeks before hawthorn host races, with emergence peaks from 4 to 5 weeks apart. Since females are likely to develop and retain host fidelity after oviposition has started (Prokopy et al. 1982a,b), it is reasonable to suppose host adaptation for domestic fruits that mature before hawthorn is more likely than for fruits that mature after hawthorn. Accordingly, adaptation to early-maturing apples grown in much of eastern North America and to cherries in Utah is more likely than adptation to the hard apple varieties that mature in late summer.

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NEW RECORDS FOR *MONOTROPA HYPOPITHYS* (ERICACEAE) FROM COLORADO

William Jennings[1], Loraine Yeatts[1], and Velma Richards[1]

ABSTRACT.—*Monotropa hypopithys* L., rarely collected in Colorado, was taken five times during 1984. Coupled with previous collections, it is now known from 10 Colorado counties. The cool, moist August of 1984 may have contributed to its apparent ubiquity.

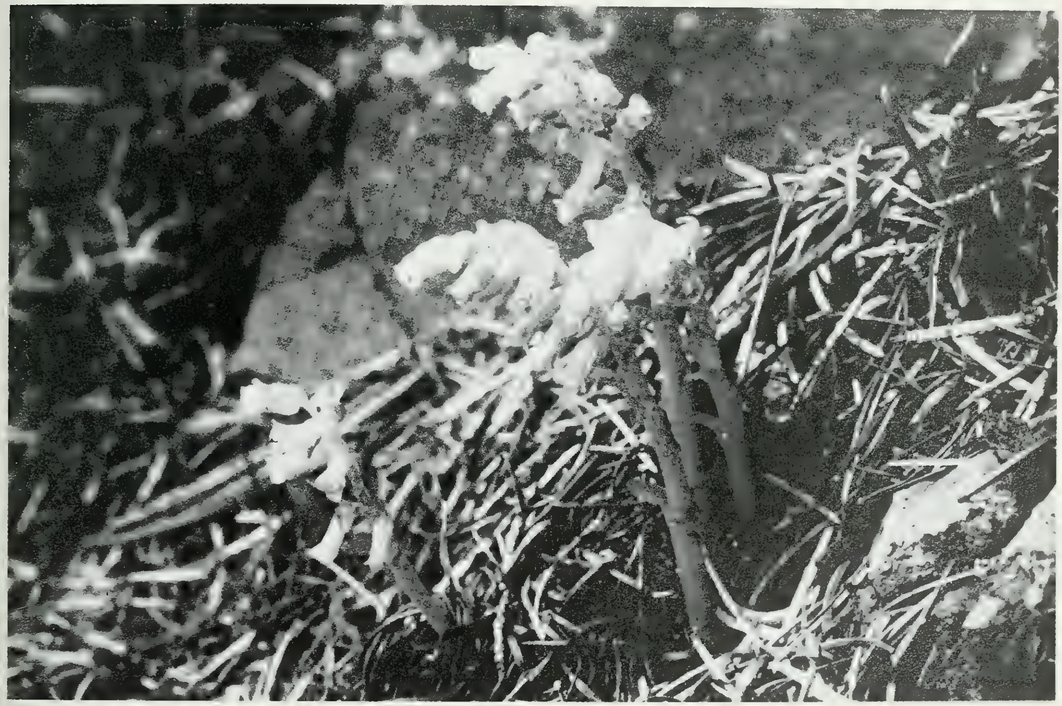

Fig. 1. Photo: *Monotropa hypopithys* L. in habitat.

The saprophytic plant *Monotropa hypopithys* L. (Ericaceae), popularly known as pinesap (Fig. 1), has been described as rare in Colorado (Harrington 1954, Weber 1976). The Colorado Natural Heritage Inventory (Peterson 1984) maintains it on the list of Plant Species of Special Concern as a plant that may be in danger of extirpation from Colorado because of the scarcity of occurrence. A survey of three regional herbaria shows a paucity of specimens (four at University of Wyoming, two at Colorado State University, and three at University of Colorado), generally supporting its characterization as a rare plant.

During the summer of 1984, *M. hypopithys* was collected by us in five Colorado counties: Routt, Jackson, Douglas, Mineral, and Las Animas. These new observations, coupled with our previous sightings and collections and the existing herbarium specimens, show that *M. hypopithys* is probably more widespread than previously thought. As shown on the map (Fig. 2), it is now known from 10 counties in Colorado. In addition, B. E. Nel-

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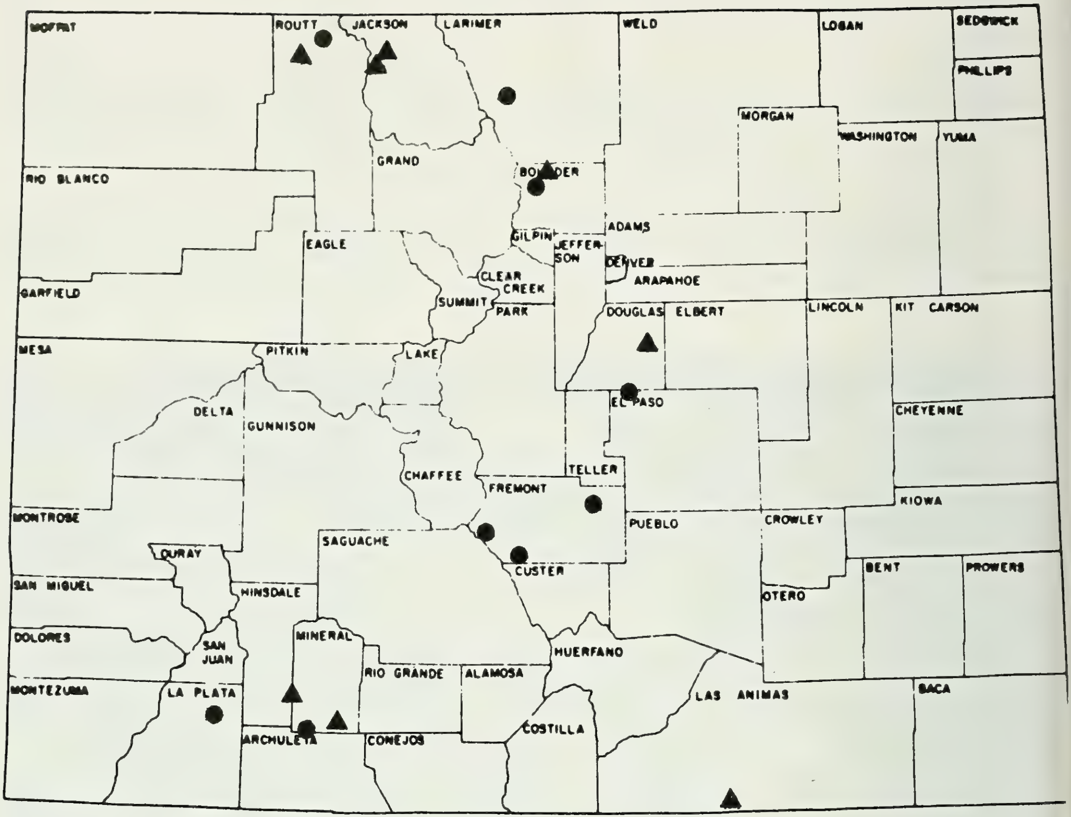
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CHEYENNE
DELTA
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CHAFFEE
FREMONT
KIOWA
MONTROSE
PUEBLO
CROWLEY
SAGUACHE
OURAY
CUSTER
BENT
PROWERS
SAN MIGUEL
HINSDALE
OTERO
DOLORES
MINERAL
SAN JUAN
HUERFANO
RIO GRANDE
ALAMOSA
MONTEZUMA
LA PLATA
LAS ANIMAS
BACA
ARCHULETA
CONEJOS
COSTILLA

Fig. 2. Colorado distribution of *Monotropa hypopithys* L.:
● Herbarium Specimens (COLO, CS, RM) (Table 1);
▲ author's collections and observations (Table 2).

son of the Rocky Mountain Herbarium at University of Wyoming concurs that it was much more widespread during 1984; he observed it in the Medicine Bow Mountains of southern Wyoming.

The details on existing herbarium specimens are presented in Table 1; the details of our recent observations are tabulated as Table 2. All specimens were deposited at the Kathryn Kalmbach Herbarium of Denver Botanic Gardens and/or University of Colorado—Boulder. Photographs are in our collections.

Habitat for *M. hypopithys* is in damp coniferous woods where there is little understory vegetation, but rather forest duff composed of rotting logs, twigs, and conifer needles. Usually such a habitat is found on a north-facing slope at high elevation. Most of our collection or observation sites follow this characterization. The 1983 and 1984 Jackson County sites, the 1974 and 1979 Boulder County sites, the 1984 Las Animas County site, and the 1980 Hinsdale County site were all on moist, heavily wooded, northeast-, north-, or northwest-facing slopes above 8,000 ft (2,400 m). The 1984 Mineral County site was on a steep densely forested, but southwest-facing slope. The 1984 Routt County site was on flat ground in open woods, with a number of rotting logs. This site was adjacent to a national forest campground and presumably much of the deadwood had been gathered as firewood, contributing to the openness. However, the 1984 Douglas County site was a dry but heavily wooded hillside at 6,800 ft (2,070 m) with an easterly exposure—but the most likely habitat compared with the surrounding area.

The plant was associated with pinedrops (*Pterospora andromedea* Nutt.), another ericad, and with coralroot orchids (*Corallorhiz* sp.), which are usually in fruit when *M. hypopithys* is at its prime. At the Jackson County sites the plants were associated with *Rhodo*

TABLE 1. Herbarium specimens of *Monotropa hypopithys* L. (CS, RM, COLO).

County	Location	Date	Collector and accession number
Douglas or El Paso*	Palmer Lake	– August 1914	Bethel (CS33885)
Larimer	East Twin Lake	3 August 1974	Kopp (CS26043)
Mineral or Archuleta*	N of Pagosa Springs	14 August 1917	Payson (RM101307)
Fremont	Sec 31 T47N R12E	20 August 1938	Lemmon (RM-USFS)
Fremont	Sec 13 T47N R10E	25 August 1960	Gierisch (RM-USFS)
La Plata	Sec 30 T37N R6W	25 July 1934	Loughridge (RM-USFS)
Fremont	Phantom Canyon	21 August 1971	Howard (COLO256444)
Boulder	Sec 23 T2N R73W	28 July 1966	Clark & Arp (COLO214312)
Routt	Big Red Park	7 September 1969	Stevenson (COLO244531)

*County of collection not listed on herbarium sheet.

TABLE 2. Collections and observations of *Monotropa hypopithys* L.

County	Location	Date	Collector
Douglas	Castlewood Canyon	26 July 1984	WFJ (specimen)
Jackson	T9N R82W Sec 14/15	4 August 1984	WFJ (specimen)
Las Animas	NW of Lake Dorothy	25 August 1984	WFJ (specimen)
Routt	T10N R86W Sec 11	2 September 1984	WFJ (specimen)
Boulder	West of Peaceful Valley	3 August 1974 5 August 1979	WFJ (photos)
Jackson	Helena-Grizzly Trail near Bear Creek	16 August 1983	LY (specimen)
Mineral	T37N R1E Sec 8	25 August 1984	LY & VR (specimen)
Hinsdale	Piedra River T37N R2W Sec 5	18 August 1980	LY (photo)

dendron albiflorum Hooker; at the Mineral County site with *Goodyera oblongifolia* Raf. and *Pyrola picta* Smith ex Rees; and at the Las Animas County site with *Goodyera repens* (L.) R. Brown, *G. oblongifolia*, and *Corallorhiza* sp.

Described by Harrington as "pink or reddish, sometimes yellowish," all degrees of coloration from red through pink to a creamy yellow have been noted by us. In fact, such variations can be seen at a single site, in plants only a few feet apart.

The reason for the seemingly ubiquitous nature of *M. hypopithys* during 1984 is not known. Perhaps our extensive travel in Colorado during 1984 had something to do with it. It may be that the atypically moist, cool August of 1984 permitted the plants to stay fresher longer than normal, leading to an apparent but not necessarily real increase in the population. As a saprophyte, the plant is quite fleshy. In a warmer, dryer August, *M. hypopithys* changes from red or yellow to crispy-brown rather quickly and effectively disappears into the featureless brown duff of the forest floor.

Whatever the reason for its widespread appearance during 1984, it seems clear that the plant isn't really rare (only during some years), but occurs in scattered localities in many forested mountainous counties.

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TREE DENSITIES ON PINYON-JUNIPER WOODLAND SITES IN NEVADA AND CALIFORNIA

Susan Koniak[1]

ABSTRACT.— The densities of singleleaf pinyon and Utah juniper trees in four diameter classes (1–9, 10–19, 20–29, and ≥ 30 cm) were measured on 522 plots of 1/10 ha each throughout the Great Basin. Density distribution patterns of pinyon and juniper varied with aspect, elevation, and eastern (EGB) versus western Great Basin (WGB) locations. On most locations north and, to a lesser extent, west slopes supported higher densities of pinyon than south and east slopes, with high relative densities of small diameter trees on north slopes and large diameter trees on west slopes. Pinyon densities were higher on EGB than on WGB sites and on higher elevation than on lower elevation sites. Juniper densities were higher on EGB than on WGB sites and on lower elevation than on higher elevation sites. Juniper densities on low-elevation WGB sites were higher on south and west aspects than on north and east, with higher relative densities in the 20–29 cm diameter class than in other diameter classes. On low elevation EGB sites, east and south slopes supported higher juniper densities than did north and west slopes, with comparatively higher relative densities in the 10–19 cm diameter class. Differences in relative densities between diameter classes were not significant among aspects on high elevation sites.

Singleleaf pinyon-Utah juniper (*Pinus monophylla* and *Juniperus osteosperma*) woodlands occupy about 7.1 million ha within the Great Basin (Tueller et al. 1979). These woodlands are most prevalent on mountain slopes above sagebrush-dominated (primarily *Artemisia tridentata tridentata*) communities of the valley bottoms. The woodlands may extend to the mountain tops or to the lower edge of high-elevation sagebrush (primarily *Artemisia tridentata vaseyana*) communities. Few studies have recorded the effect of aspect and elevation on tree distribution in mature pinyon-juniper woodlands (West et al. 1978, Tueller et al. 1979, Cooper et al. 1980, Tausch et al. 1981). This paper reports on variations in tree densities by diameter class over four aspects, two elevation classes, and two sections of the Great Basin.

FIELDS METHODS AND DATA ANALYSIS

In 1981 and 1982, the densities of pinyon and juniper trees in four diameter classes (1–9, 10–19, 20–29, and ≥ 30 cm) were determined on 522 plots of 1/10 ha each, on 20 areas in Nevada and California (Fig. 1). Tree diameters were estimated at stump height. Densities were obtained on plots selected for another study in which vegetation on wildfires of various ages and adjacent unburned sites were recorded. Data from 112 unburned woodland sites were combined with data from 410 wildfire sites for analysis. On wildfire sites the number of remnant tree skeletons was recorded to reflect tree densities. The smallest diameter class may be underestimated on burned sites. All wildfire sites were burned within the last 30 years, with 76% of those sites burned within the last 15 years. We sampled only those sites in which pinyon was or had been the dominant species and the understory had been or was assumed to have been (by extrapolation from conditions on adjacent sites) substantially reduced by tree competition. Each plot contained a minimum of 10 trees, 5 with diameter ≥ 20 cm. In each of the 20 areas, tree cores were taken from a minimum of 3 mature dominant pinyon trees on the unburned sites for a total of 91 cores. Plot elevations ranged from 1,585 to 2,280 m, and average slope for each area ranged from 16% to 64%. Estimated annual precipitation for each area ranged from 20 to 33 cm.

Following Cronquist et al. (1972), the sampled areas were divided into three groups—the Reno (or western) section containing 10 sampled areas and 313 plots, the central Great

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[1] At the time of this research, the author was with the Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Ogden, Utah 84401, located at Reno, Nevada.

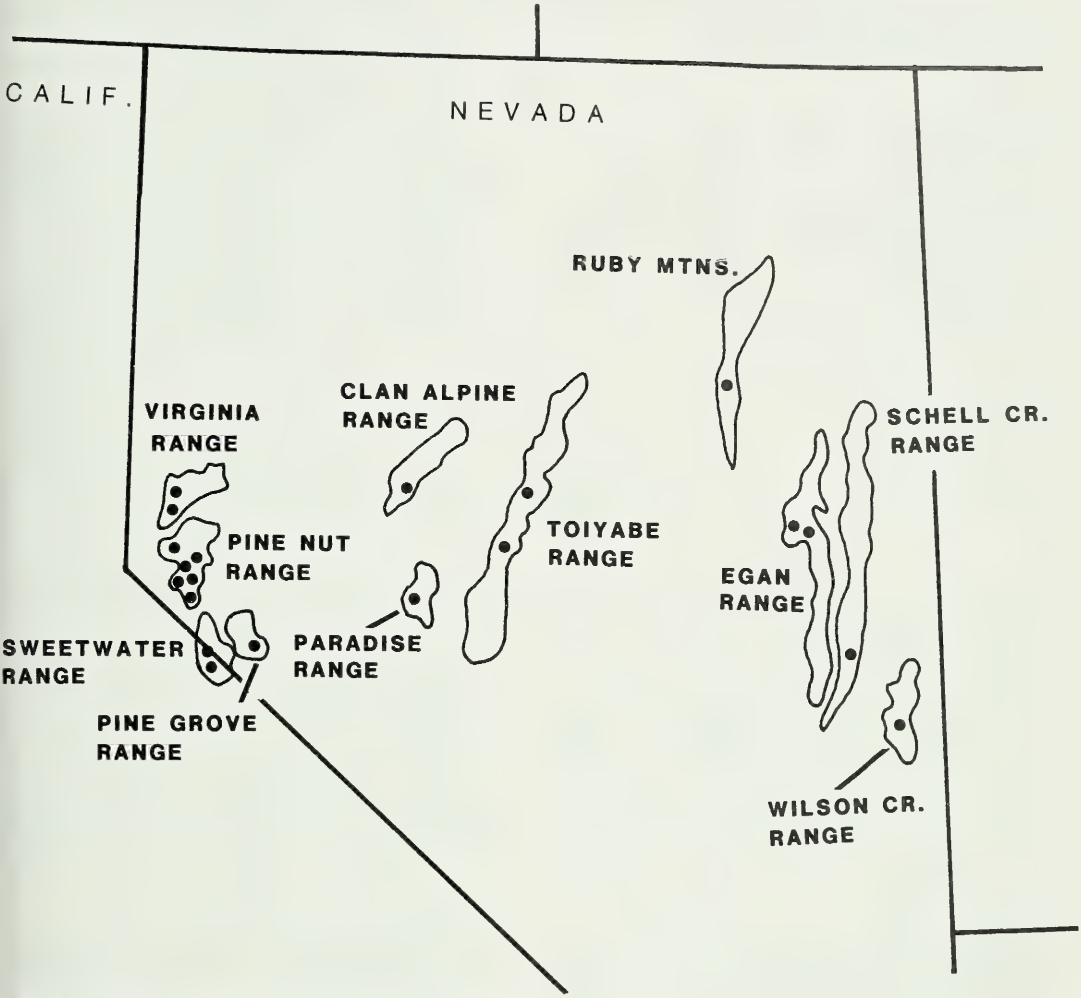

CALIF.
NEVADA
RUBY MTNS.
CLAN ALPINE RANGE
VIRGINIA RANGE
SCHELL CR. RANGE
PINE NUT RANGE
TOIYABE RANGE
EGAN RANGE
PARADISE RANGE
SWEETWATER RANGE
PINE GROVE RANGE
WILSON CR. RANGE

Fig. 1. Location of 20 study sites in Nevada and California.

Basin and Tonapah sections (or central section) containing 5 sampled areas and 117 plots, and the Calcareous Mountain (or eastern Great Basin) section containing 5 sampled areas and 92 plots. Similarity of tree distribution between aspects in the western and central sections on both high- and low-elevation sites justified combining the data from these two sections for analyses (collectively designated as the western Great Basin section).

One-way and two-way analyses of variance were used to compare the number of trees per plot (density) and the percent of the total tree density in each diameter class (relative density) on eastern and western Great Basin sites; on north, south, east, and west aspects; and at high and low elevations. In the eastern Great Basin (EGB), the point selected to differentiate between high and low elevations was 2,160 m compared to 2,040 m in the western Great Basin (WGB). The difference in elevational division reflects sectional differences in woodland belt width and elevational range. The lowest site measured in the eastern section was 2,030 m compared to 1,585 m in the western section.

RESULTS AND DISCUSSION

The average age of the pinyon trees in each area sampled ranged from 72 to 159 years. The median age of all pinyon trees sampled was 96 years, with 51% of the trees sampled falling within the 70–110-year age group. Age differ-

TABLE 1. Comparison of tree densities (number of trees per 1/10 ha) between eastern and western Great Basin sites, high and low elevations, and four aspects.

Location	Aspect			
	North	East	South	West
Total tree density:				
Eastern (high elevation)	28.0^{abc}[1]	33.2^{a}	29.0^{abc}	29.8^{ab}
Eastern (low elevation)	30.2^{ab}	28.0^{abc}	30.7^{a}	27.5^{abc}
Western (high elevation)	23.6^{bc}	17.6^{e}	17.2^{de}	19.7^{de}
Western (low elevation)	22.2^{cd}	17.0^{e}	18.5^{de}	19.8^{de}
Pinyon tree density:				
Eastern (high elevation)	24.4^{abc}	27.4^{a}	22.6^{abc}	24.7^{ab}
Eastern (low elevation)	25.0^{ab}	16.5^{bcd}	19.3^{abcd}	20.5^{abcd}
Western (high elevation)	23.1^{ab}	17.2^{cd}	16.9^{cd}	19.3^{bcd}
Western (low elevation)	21.4^{ab}	16.4^{cd}	15.2^{d}	17.3^{cd}
Juniper tree density:				
Eastern (high elevation)	3.6^{cd}	4.8^{bcd}	6.4^{bc}	5.1^{bcd}
Eastern (low elevation)	5.2^{bcd}	11.5^{a}	10.5^{a}	6.9^{b}
Western (high elevation)	0.5^{e}	0.4^{e}	0.4^{e}	0.4^{e}
Western (low elevation)	1.0^{e}	0.8^{e}	3.3^{d}	2.5^{d}

[1] Means followed by the same letters a, b, c, d, or e do not differ significantly at $P < 0.05$. Each block is a separate analysis.

ences were not apparent between EGB and WGB. Most stands appeared to have established in the mid- to late 1800s or early 1900s (Tausch et al. 1981). During this period pinyon-juniper woodlands were heavily harvested to supply fuel and charcoal for the mining industry. Subsequent regrowth, concurrent with limited harvesting and intensive fire control, has tended to create large woodland areas dominated by trees of roughly equal age (Lanner 1980, Young and Budy 1979). Intensive livestock grazing, which reduced competition from herbaceous and shrubby plant species, may also have contributed to the increase in tree density and dominance during this period (Blackburn and Tueller 1970). Unburned stands exhibited few signs of major disturbance from this period until the present, suggesting that the burned areas may also have been relatively undisturbed until wildfire occurred.

Tree densities on all aspects for both high- and low-elevation classes were higher on EGB sites than on WGB sites, with differences being smallest among north aspects (Table 1). Tree densities were not different between aspects or between elevation classes on EGB sites nor between high- and low-elevation WGB sites of the same aspect. In the WGB, tree densities were higher on north slopes than on other aspects for both high and low elevations.

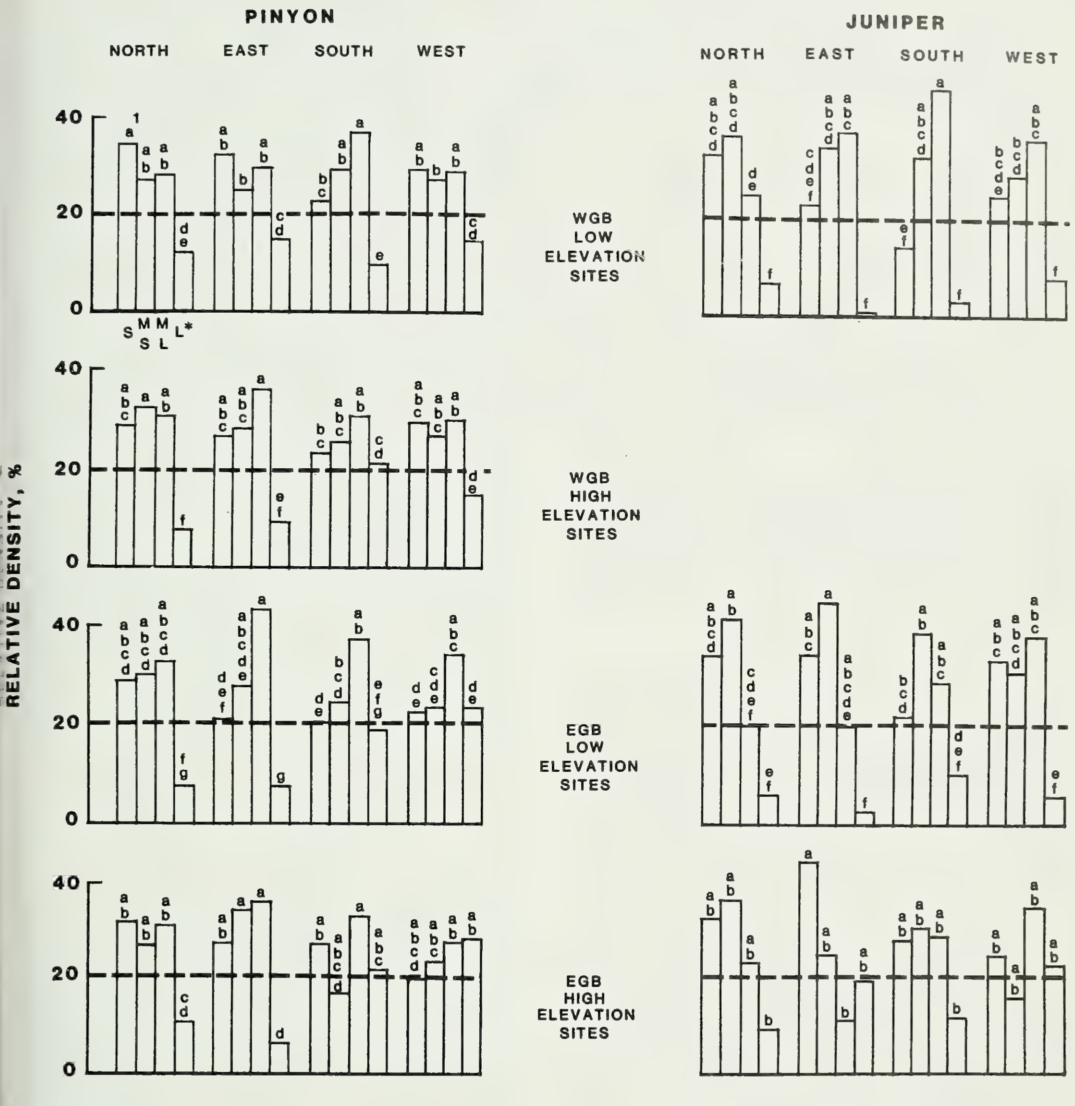
Pinyon Densities

Pinyon densities were generally highest on high-elevation sites and north aspects (Table 1). Cooler, moister environments and longer periods of snow cover were characteristic of these sites. Pinyon densities were also higher in the EGB than WGB, corresponding to higher average annual precipitation and lower average annual temperatures in the EGB (NOAA 1983). Pinyon dominance, contrary to total tree density, was greatest in the WGB, where summer precipitation is at a minimum. In both EGB and WGB the second highest pinyon densities were consistently found on west aspects.

High-elevation EGB sites, unlike other locations, supported higher pinyon densities on east aspects than on north aspects. This may be related to the higher number of storms from the east in the EGB than in the WGB. However, the same relationship is not evident at lower elevations.

Juniper Densities

The density of Utah juniper was greatest in the EGB, on low-elevation sites, and on south slopes (Table 1). The frequency distribution patterns indicate that juniper dominance is positively correlated to higher summer precipitation and greater diurnal fluctuation of soil moisture and temperature. There was some evidence that the higher incidence of paleozoic sedimentary soil parent material in the EGB may be related to higher densities of juniper, but more comprehensive study is required to clarify the relationship. Higher an-



[1] Within each block of 16 bars, bars with the same letters a,b,c,d,e,f, or g do not differ significantly at $P < 0.05$.

*Diameter classes : S = 1-9 cm, MS = 10-19 cm, ML = 20-29 cm, L = ≥ 30 cm.
This sequence is repeated for every group of four bars.

Fig. 2. Variation in pinyon and juniper relative densities among four diameter classes, four aspects, two elevations, and two locations (WGB = western Great Basin; EGB = eastern Great Basin).

nual precipitation on EGB sites compared to WGB sites probably was not directly related to higher juniper densities, since greater juniper densities were not also evident on generally moister sites at high elevations.

Relatively high juniper densities on low-elevation west-facing slopes in the WGB and on low-elevation east-facing slopes in the EGB may be related to differences in prevailing summer weather patterns (Houghton 1969, Presley 1978). In the WGB summer storms are infrequent and primarily originate in the west and southwest. In the EGB summer storms occur frequently, often originating in the southeast. Influence of aspect on juniper densities was less at high elevations, resulting in approximately equal tree densities on all aspects.

Relative Densities According to Diameter Classes—Pinyon

On north aspects, differences between relative densities (percentage of total tree density in each diameter class) of pinyon in the 1–9, 10–19, and 20–29 cm diameter classes were small except on low-elevation WGB sites (Fig. 2). On these sites a higher proportion of pinyon trees were in the 1–9 cm class. Relative densities in the ≥ 30 cm class were significantly lower than those in the other diameter classes. North slopes, compared to other aspects, tended to have higher proportion of pinyon trees in the 1–9 and 10–19 cm diameter classes.

On east aspects the highest pinyon relative densities were generally in the 20–29 cm diameter class and the lowest in the ≥ 30 cm class. Low-elevation WGB sites deviated from this pattern with high relative densities in the 1–9 cm class. Compared to other aspects, east-facing slopes tended to have higher proportions of pinyon trees in the 20–29 cm classes.

South aspects, like east slopes, had higher proportions of pinyon trees in the 20–29 cm diameter class than in the other classes for all locations. Unlike the distribution of pinyon on east aspects, south aspects also supported relatively high pinyon densities in the ≥ 30 cm diameter class at most locations. South slopes rivaled east slopes for highest relative densities in the 20–29 cm class and west slopes for highest relative density in the ≥ 30 cm class.

On west aspects, pinyon distribution differed substantially between WGB and EGB sites. On WGB sites relative densities in the 1–9, 10–19, and 20–29 cm diameter classes were not significantly different, and those in the ≥ 30 cm class were significantly lower. On EGB sites pinyon relative densities tended to be highest in the 20–29 and ≥ 30 cm classes and lowest on the 1–9 and 10–19 cm classes. Compared to other aspects, west-facing slopes consistently supported high proportions of trees in the ≥ 30 cm diameter class.

Relative Densities According to Diameter Class—Juniper

Because juniper densities were very low on high-elevation WGB sites, these data were deleted from the analysis and discussion of density distribution patterns among diameter classes. Juniper relative densities in the ≥ 30 cm diameter class were lower than in the other classes for all locations except high-elevation EGB east and west slopes. On north slopes juniper relative densities were consistently higher in the 1–9 and 10–19 cm diameter classes than in the 20–29 cm class. On west aspects juniper relative densities were consistently higher in the 20–29 cm class than in the other classes. Distribution of juniper among the three smaller diameter classes on east and south aspects exhibited no consistent patterns. Relative densities in the two smaller classes tended to be higher on north and east slopes than on other aspects. South and west aspects frequently supported higher juniper relative densities in the 20–29 and ≥ 30 cm class than did north and east aspects.

Elevational and Sectional Effects on Distribution Patterns

The basic patterns of pinyon and junipe distribution among diameter classes wer similar between high and low elevation (Fig 2). Several trends were apparent, but the were generally not significant. On WGB site variation in relative densities between elevation classes was not consistent between aspects. On EGB sites all aspects generally exhibited an increase in pinyon in the 1–9 and ≥ 30 cm diameter classes with increasing elevation, whereas middiameter class relative densities decreased. Juniper relative densities i the ≥ 30 cm diameter class also tended t increase at higher elevations on EGB sites accompanied by a decrease in the 10–19 c class. Consistently larger trees at high elevation EGB sites may indicate older stands o better growing conditions at these elevations

Distribution patterns of pinyon and junipe among diameter classes were similar betwee EGB and WGB sites (Table 2). For bot pinyon and juniper, distribution patterns o north aspects were almost identical betwee EGB and WGB sites. On other aspects ther

TABLE 2. Comparison of pinyon and juniper relative densities on eastern (EGB) and western Great Basin (WGB) sites among four aspects and four diameter classes.

Aspect	Diameter class and location							
	1–9 cm		10–19 cm		20–29 cm		≥ 30 cm	
	WGB	EGB	WGB	EGB	WGB	EGB	WGB	EGB
Pinyon								
North	32.8	30.5	28.9	28.8	28.9	31.7	10.7	10.1
East	30.3	24.8	26.0	31.6	32.1	38.1	13.6	6.1
South	23.4	23.0	28.1	22.2	34.4	35.0	14.0	19.6
West	29.7	21.3	26.6	23.3	29.2	30.9	15.5 *	24.4
Juniper								
North	32.7	33.4	38.5	39.3	24.4	20.9	5.0	6.4
East	21.2	39.9	42.3	33.9	33.9	14.4	0.0 *	11.8
South	15.1	24.4	28.1	36.3	54.8 *	28.6	2.1 *	10.8
West	28.4	27.2	29.3	21.2	36.0	36.9	6.8	14.7

*Pairs denoted by an asterisk (*) are significantly different at $P < 0.05$.

was wider variation; however, few of these differences were significant. WGB south slopes supported significantly greater juniper relative densities in the 20–29 cm diameter class than did EGB south slopes. Pinyon relative densities on west-facing sites and juniper relative densities on south-facing and east-facing sites were significantly higher in the ≥ 30 cm class on EGB sites than on WGB sites. The consistently higher proportion of trees in the ≥ 30 cm class on EGB sites than on WGB sites may indicate better growing conditions or an earlier onset of stand establishment.

Major Distribution Patterns Among Diameter Classes

Sites with the highest total juniper densities (i.e., low elevation south and east EGB sites and low elevation south and west WGB sites) displayed different distribution patterns among diameter classes (Fig. 2). In the WGB, regeneration appeared to have been greatest in the early tree stage of the successional cycle, after the first generation of trees had reached seed-bearing age. Subsequent regeneration may have been limited by competitive interaction for water, nutrients, and space, or by infrequent environmental conditions conducive to seed germination and seedling survival. In the EGB the highest tree establishment rates apparently occurred later in the successional cycle than they did in the WGB. This may have been because environmental conditions were favorable during this period, producing an unusually high regeneration rate. Or perhaps the natural accretion of trees into seed-bearing age, the continued capability of the sites to support new trees, and climate favorable to tree establishment may have yielded progressively higher proportions of small diameter trees, diminishing only in recent years when either adverse environmental conditions or competition limited regeneration. Interspecific competition may also have affected density distribution among diameter classes. For example, high proportions of pinyon in the larger diameter classes on low-elevation EGB sites may indicate early domination by pinyon and subsequent delayed establishment of juniper.

Sites with the highest pinyon densities, north and high-elevation EGB east aspects, displayed similar distribution patterns among diameter classes. Pinyon regeneration on these sites remained high after tree establishment and had not decreased substantially in recent years. The relatively low proportions of trees in the ≥ 30 cm diameter class on these sites may indicate either that competition between large numbers of small-diameter trees restricted or delayed the number of trees attaining substantial girth or that stand establishment occurred later on these sites than on other sites. Historically, north and east slopes may have been exposed to a greater frequency and severity of wildfires than have other aspects because of the generally higher biomass to carry fire. Fire suppression policies in the early 1900s allowed the invasion of many sites previously dominated by shrub disclimax communities. Stand establishment on invaded shrub areas would occur slower than stand establishment after tree harvesting because cut-over areas generally retain numerous small diameter trees. Greater competition from perennial species (Koniak 1985) on these slopes may also delay tree establishment. Neither the tree competition nor the late stand establishment hypotheses are clearly supported by tree diameter and age data in this study or in the literature (Meeuwig 1979, Cooper et al. 1980). More comprehensive study is needed to clarify the underlying processes.

Of the four aspects, west slopes consistently supported the second highest pinyon densities at all locations. Less competition or earlier stand development with less disturbance or both may explain the disproportionately high number of trees in the ≥ 30 cm diameter class on west slopes. EGB west slopes supported higher proportions of pinyon trees in the ≥ 30 cm diameter class than WGB west slopes at both high and low elevations. In the WGB tree establishment has remained high on west slopes. On EGB west slopes competition from large-diameter trees may have restricted regeneration, limiting the proportion of pinyon trees in the smaller diameter classes.

Distribution of pinyon and juniper over aspect, elevation, and eastern versus western Great Basin locations tended to be negatively correlated. However, variations in relative density distribution between diameter classes were often similar. For both pinyon and juniper, north and, to a lesser extent, east aspects tended to support high relative densities of small-diameter trees, whereas south and west aspects tended to support high relative densities of large-diameter trees. Of the diameter classes, relative pinyon and juniper densities were generally lowest in the ≥ 30 cm class. For both pinyon and juniper, relative densities in the ≥ 30 cm class tended to increase with elevation, especially on south and west aspects. One striking difference in the diameter class distribution is the consistently lower proportion of juniper trees in the ≥ 30 cm classes compared to pinyon trees. Juniper appear to be more sensitive to competition than pinyon (Meeuwig 1979) and may be slower to establish in communities where both species are represented.

Most stands sampled had a substantial proportion (20%–35%) of both pinyon and juniper trees in the 1–9 cm diameter class, indicating these woodlands are still in the formative stages of stand renewal (Meeuwig and Cooper 1981). At what point equilibrium with the natural environment will be reached, and the nature of the stand at that time, are largely matters of conjecture. Recording the process, however, will have value in our understanding the dynamics of this system.

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8-86 650 25552

ISSN 017-3614

The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 46 | 30 April 1986 | No. 2

BIOLOGY OF RED-NECKED PHALAROPES (*PHALAROPUS LOBATUS*) AT THE WESTERN EDGE OF THE GREAT BASIN IN FALL MIGRATION

Joseph R. Jehl, Jr.[1]

ABSTRACT.—Large numbers of Red-necked Phalaropes migrate overland across the Great Basin in fall, occurring commonly at highly saline lakes. Migrants occur at Mono Lake, California, from mid-July to mid-October. The earliest migrants are adult females, followed several weeks later by adult males, and finally by juveniles. Adults make up ca 75% of the population, with males outnumbering females by 5:4. From 1980 through 1984 an estimated 52,000–65,000 birds passed through the area each year, except in 1983, when only 36,000 were recorded. The low number might be attributable to high mortality on oceanic wintering grounds in the Southern Hemisphere in 1982 associated with the severe El Niño. At Mono Lake the phalaropes concentrate near the shore and feed almost exclusively on brine flies. The migrants neither gain much weight nor accomplish much molt during their sojourn, which suggests that the average stay is only a few days. Some aspects of the molt pattern differ from those reported elsewhere.

After the breeding season, many Red-necked Phalaropes (*Phalaropus lobatus*) migrate from breeding grounds in the arctic regions of the New World to pelagic wintering areas in the equatorial Pacific Ocean. Substantial numbers, presumably from the west and central Canadian Arctic, move overland, and each fall hundreds of thousands occur in the Great Basin of the western United States. Concentrations exceeding one million individuals have been estimated at Great Salt Lake, Utah (Kingery 1982). Thousands also occur at Lake Abert, Oregon (K. Boula, personal communication), Mono Lake, California (Cogswell 1977, Winkler 1977), and Stillwater National Wildlife Refuge, Fallon, Nevada (S. Thompson, personal communication), and arge but unestimated numbers visit the Salton Sea (McCaskie 1970, Garrett and Dunn 1981). The existence of an overland migration route in this species has long been known (e.g., Fisher 1902, Bent 1927, Grinnell and Miller 1944). What does not seem to have been appreciated, however, is that saline lakes are preferred stopping places.

This report documents the fall migration at Mono Lake, California. It is based on studies that spanned the entire fall migration period, July through mid-October, for six consecutive years (1980–1985). The major goals were to document abundance, period of occurrence, and ecological requirements of the Red-necked Phalarope and to determine the composition of the population throughout the migration period.

METHODS

Mono Lake (surface elevation 6,380 ft in 1984) is a large (ca 160 km) basin lake at the western edge of the Great Basin in east central California. It is highly saline (surface salinity 75–90 0/00 during this study) and alkaline (pH ≅ 10) and contains no fishes (see Hubbs and

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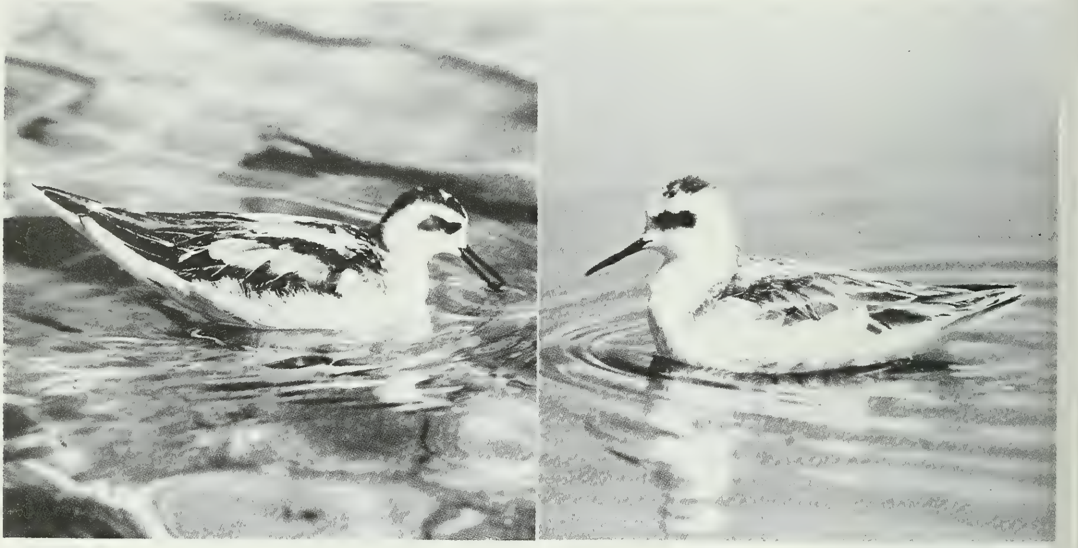

Fig. 1 Juvenile (left) and adult (right) Red-necked Phalaropes.

Miller 1948). Accordingly, the aquatic invertebrates (brine shrimp, *Artemia* sp., and brine flies, *Ephydra hians*) that provide food for the phalaropes and a few other species of migratory birds can attain great abundances.

I made behavioral observations through the entire migration period. Specimens were weighed, measured, and examined for molt and external parasites. Stomach contents were identified using a binocular microscope. Fat-free weights were determined using standard ether-extraction techniques. I estimated the percentage of molting feathers in each of the body tracts and determined molt scores for primaries and rectrices. A value of 0 is given to an unmolted feather, 5 for one that has been replaced, and 1 to 4 for intermediate stages (e.g., Morrison 1976). Thus, a bird that has replaced all its primaries and rectrices would receive scores of 100 (i.e., 5 × 10 primaries × 2 wings) and 60 (5 × 12 rectrices).

CENSUSING.—Because of their localized distribution and preference for nearshore habitat, phalaropes are relatively easily censused. Counts from a boat cruising ca 400 m offshore will reveal nearly all birds, except those hidden behind tufa formations. As the migration period progresses, it is not uncommon to find flocks of 30–400 birds 2 km or more from shore; these can be detected by routine transects. Censusing by boat produces consistent and replicable results. I estimate that errors did not exceed 15%–20%, even when populations were large. For example, replicate censuses of birds on the eastern half of Mono Lake on 31 August and 1 September 1981 resulted in estimates of 6,800 and 7,053 birds, a difference of 3.5%

AGE AND SEX RATIOS.—Male Red-necked Phalaropes bear the responsibility for incubation and caring for the young. Females leave the breeding grounds about the time young hatch and are followed by the adult males several weeks later and, finally, by the juveniles (Hildén and Vulanto 1972). At Mono Lake the migration period of each of these groups is protracted, perhaps because: (1) the population is composed of birds from several nesting areas, where the start of breeding may vary by a week or more; (2) the species is polyandrous, and females that obtain more than one mate remain on the breeding grounds longer than those that obtain a single mate; (3) and males that lose their eggs or young migrate earlier than successful nesters.

Sex ratios in adults usually cannot be determined in the field because plumage differences, although pronounced on the breeding grounds, dull with the onset of molt. Estimates in this report are derived largely from specimens collected with no conscious bias and are supplemented by banding data (Winkler 1977). Age ratios, however, can be determined by plumage (Fig. 1; Prater et al. 1977)

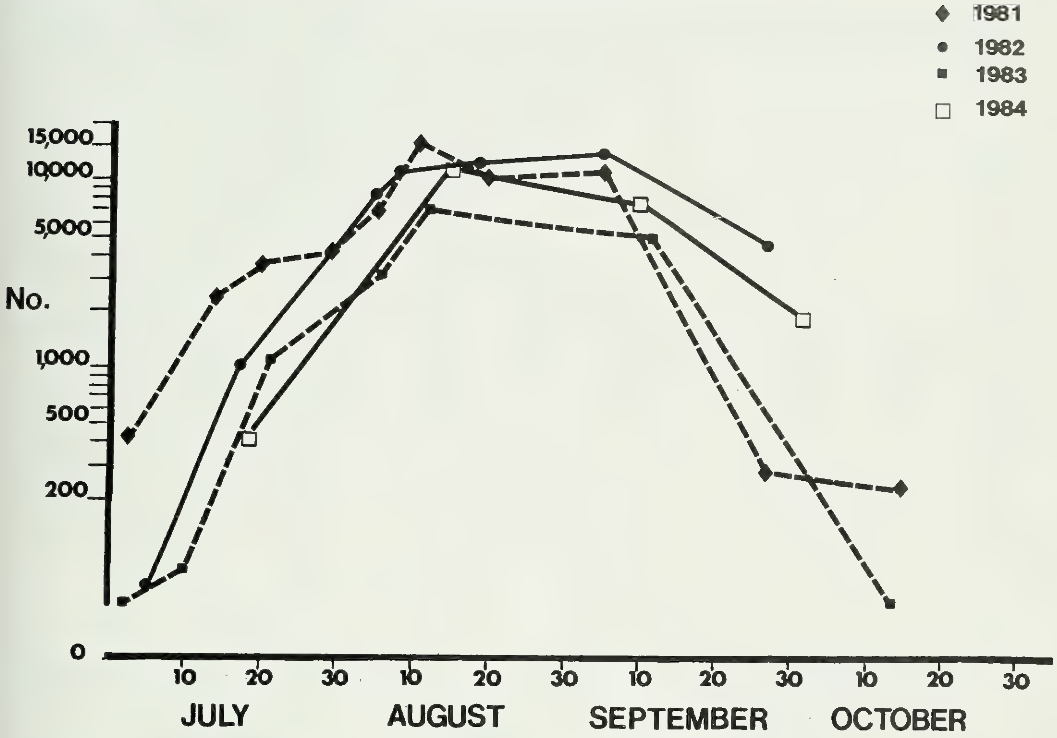

Fig. 2. Population size of Red-necked Phalaropes at Mono Lake, California, 1982–1984.

until mid-September, or later. Because the distribution of adults and juveniles is not necessarily similar, I determined age ratios in several areas of the lake, attempting to achieve a minimum total sample size of 100. Data obtained in that manner were similar to these obtained by collecting.

RESULTS

CHRONOLOGY.—In my experience, only small numbers of the Red-necked Phalarope pass through the Mono Basin each spring. I have seen flocks totaling 200 birds on several occasions on dates ranging from 30 April to 24 May, with a maximum of 800–1,000 on 13 May 1984. That much larger numbers may occur occasionally can be inferred from Ryser's (1985) report of thousands killed near Reno, Nevada, in mid-May 1964 (see also Gaines 1977). One or two may summer in some years. The few birds that appear in late June are often molting heavily, which suggests that they may not have reached the nesting areas; certainly they could not have bred. Usually there was no significant influx of migrants until the last third of July, although in 1981 more than 2,000 were present by mid-July (Fig. 2). Numbers increase through early August, peak near 10 August at ca 12,000 individuals, and remain high for the next month. A decrease is evident by 10–15 September; by early October fewer than 200 remain; and by the last third of October the species has departed. The latest dates on which phalaropes were present (based on irregular surveys) were 17 October 1980, 9 October 1981, 21 October 1982, and 14 October 1983.

Only once did I see migrants depart. On 6 August 1982, four flocks totaling 450 birds left the mouth of a freshwater creek where they had been bathing, climbed high toward the Sierra Nevada, and disappeared to the west. This suggests that some migrants may move directly toward the Pacific Ocean.

COMPOSITION OF THE POPULATION.—Adult females predominated among the early migrants (Fig. 3). The rapid population increase in late July (Fig. 2) results from the arrival of postbreeding males. By late July adult females composed fewer than half the popula-

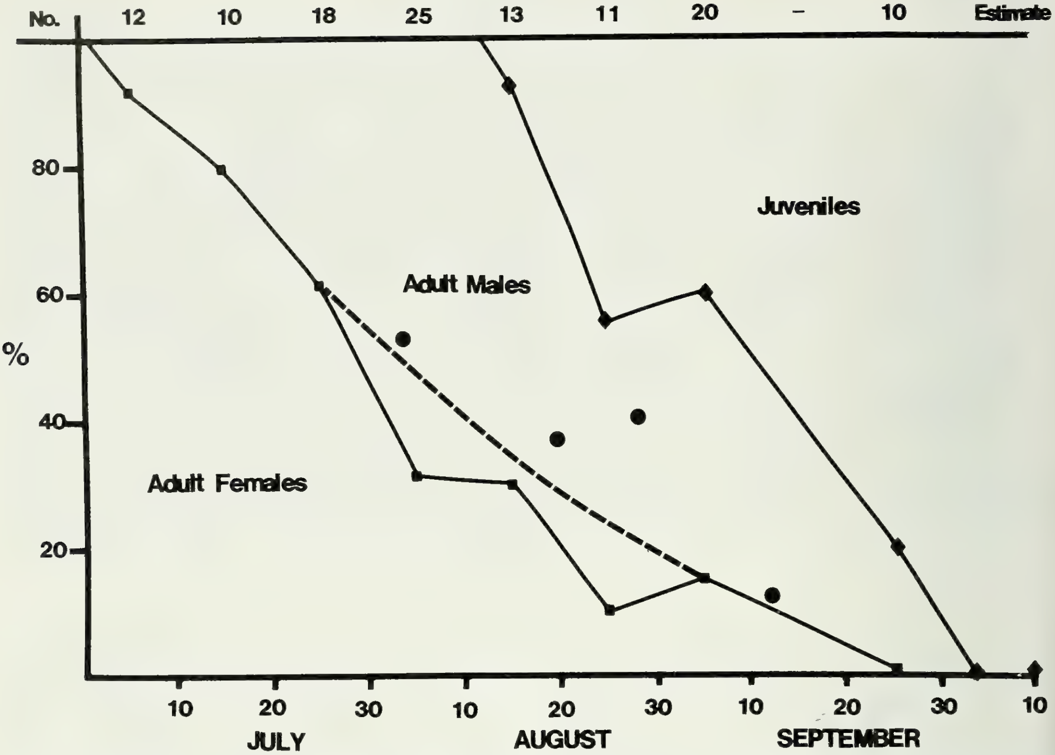

Fig. 3. Age and sex ratios of Red-necked Phalaropes based on specimens collected from 1980 through 1982. The percentage of adult females determined by banding studies (Winkler 1977) is shown by ●. The dotted line shows the inferred average percentage of adult females from late July through mid-September.

tion, and their abundance decreased through the remainder of the fall. Juveniles began arriving in mid-August (earliest 13 August 1980, 10 August 1981, 2 August 1982, after 6 August 1983), predominated by the first of September, and composed virtually all the population by early October.

SIZE OF THE POPULATION.—The size and composition of the population at major phases of the migration period are shown in Table 1. This species does not use Mono Lake either as a molting or staging area (see below) and, because the arrival period of each age and sex class is protracted, I infer that the average stays of most migrants ranged from 5 to 14 days (see also Evans 1984, Kersten and Smith 1984). Short stop-overs were also suggested by weight data (see below). The bulk of the migration for any age and sex category is accomplished in 30 days. Assuming an average stay of 10 days, one can estimate the total population at roughly three times the sum of the peak counts in each category. If so, 52,000 Red-necked Phalaropes passed through the Mono Basin in 1981, 65,500 in 1982, 36,000 in 1983; limited data from 1980 and 1984 suggest a population similar to 1981. Although the validity of the multipliers is unknown, the census data are sufficiently accurate to show that annual differences in abundance are real.

DISTRIBUTION.—Red-necked Phalaropes are pelagic for much of the year, but at Mono Lake they tend to avoid midlake habitats in favor of shallow areas within 200 m of shore. There they congregate over shallowly submerged rock formations, which provide a substrate for pupating brine flies; brine flies of al ages are their major food.

In July migrants appear along the centra north shore, where there are large expanses o tufa-encrusted rocks. As numbers increase the population spreads laterally, and by mid August birds are found almost anywhere or the periphery where there is submerged rock

Distributional patterns were similar eacl year (Fig. 4), with two exceptions. In early September 1981 approximately 2,500 of 9,00 birds were flocking offshore, perhaps in antic

TABLE 1. Size and composition of Red-necked Phalarope populations at Mono Lake, California, 1981–1984.

	Population size			Composition^a					
	Number observed								
			Estimated	Adult Female		Adult Male		Juvenile	
	Western^b	Eastern	total	%	N	%	N	%	N
1981									
2–3 Jul	9	303	400	[95]	380	[5]	20		
14–15 Jul	805	1,070	2,050	[80]	1,640	[20]	410		
21 Jul	—	—	3,000						
24 Jul	1,100–1,200	ND	—	[60]		[40]			
29–30 Jul	550+	1,500+	3,600	[55]	1,980	[45]	1,620		
4 Aug	3,445	ND	6,000	[48]	2,880	[52]	3,120	.02	120
11 Aug	3,708	6,370	12,000	[35]	4,200	[63]	6,840	2	960
19 Aug	4,300	2,130	8,500	[33]	2,805	[47]	3,995	20	1,700
31 Aug	7,030	—	—	—		—		64	
1–2 Sep	6,800	3	9,000	[13]	1,110	[17]	1,530	70	6,300
22 Sep	50	165	250	—		[20]	50	80	200
9 Oct	—	0	20	—		—	—	100	20
Total (%)					14,995(35.8)		17,585(42.0)		9,300(22.2)
1982									
2–4 May	200	—	200						
23 Jun	2	—	2	100	2	—	—		
5 Jul	5		5	[92]	5	[8]			
11 Jul	2	—	10	[80]	8	[20]	2		
17–19 Jul	100	725	1,000+	[80]	800	[20]	200		
25–27 Jul	100	1,100	1,500	[60]	900	[40]	600		
2–4 Aug	5,540	2,900	8,500	[58]	4,930	[42]	3,570	0.2	16
6–8 Aug	5,350	2,600	10,000	[58]	5,800	[42]	4,200	0.2	16
18–19 Aug	7,020	2,630	12,000	[30]	3,600	[66]	7,920	4	480
2–3 Sep	7,360	3,550	14,000	[7]	980	[35]	4,900	58	8,120
23 Sep	4,300	192	4,800		—	[20]	960	80	3,840
21 Oct	—	5	5		—		—	100	5
Total %					17,025(32.8)		22,352(43.1)		12,477(24.1)
1983									
14 May	200	—	200						
13 Jun	1		1	100	1	—	0		
21 Jun	6		6	100	6	—	0		
4 Jul	1		10	[92]	9	[8]	1		
12 Jul	30		<50	[80]	40	[20]	10		
23 Jul	200	800	1,000	[60]	600	[40]	400		
6 Aug	2,400	500	3,200	[48]	1,536	[52]	1,664		
10 Aug	—	—	8,000^b	[42]	3,360	[58]	4,640		
21 Aug	5,748	100	6,300	[19]	1,200	[31]	1,950	50	3,150
15–16 Sep	1,800	3,000	5,000	[5]	250	[15]	750	80	4,000
12–14 Oct	2	—	<10	—	—		—	100	10
Total %					7,002(30.2)		9,415(39.0)		7,160(30.8)
1984									
3 Apr			200						
13 May			1,000						
16 Jul			400	[80]	320	[20]	80		
13 Aug			12,000	[3]	4,440	[63]	7,560	+	
7 Sep			8,000	[10]	800	[32]	2,560	58	6,400
28 Sep			2,000			[20]	400	80	1,600
Total (%)					5,560(23.0)		10,600(43.9)		8,000 (33.1%)

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[a] Percentages of age or sex classes in brackets are derived from the average for any date as shown in Figure 1. Data not in brackets are based on field observations.

[b] For convenience in censusing, the lake is divided into western and eastern sectors.

[c] Data provided by J. Bright, personal communication.

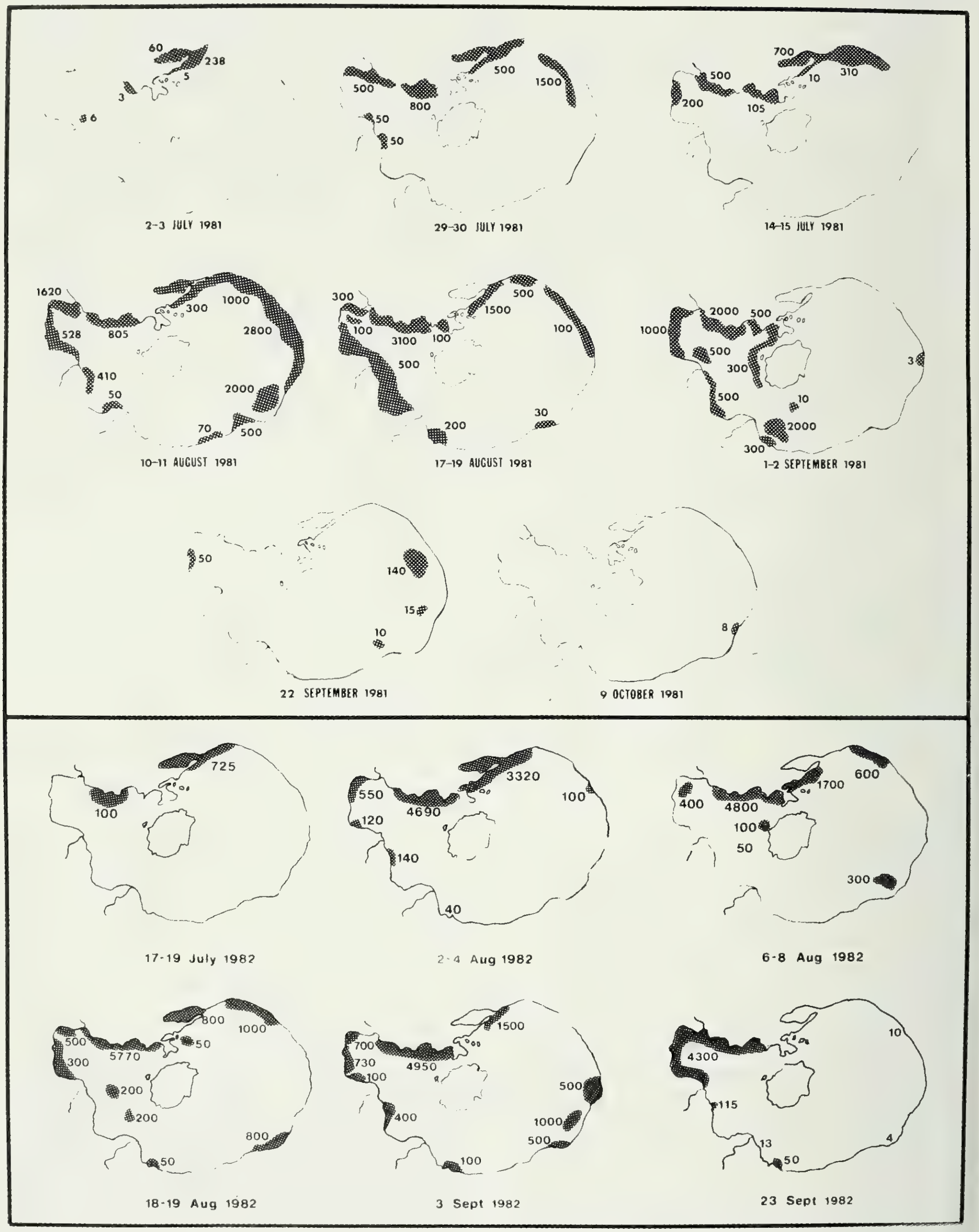
60
238
5
3
6
2–3 JULY 1981
500
1500
500
800
50
50
29–30 JULY 1981
700
310
500
10
200
105
14–15 JULY 1981
1620
1000
300
528
805
2800
410
50
2000
70
500
10–11 AUGUST 1981
300
500
1500
100
3100
100
100
500
30
200
17–19 AUGUST 1981
2000
500
1000
500
300
3
500
10
2000
300
1–2 SEPTEMBER 1981
50
140
15
10
22 SEPTEMBER 1981
8
9 OCTOBER 1981
725
100
17-19 July 1982
3320
550
100
4690
120
140
40
2-4 Aug 1982
600
1700
400
4800
100
50
300
6-8 Aug 1982
800
1000
500
50
300
5770
200
200
800
50
18-19 Aug 1982
1500
700
730
4950
100
500
400
1000
500
100
3 Sept 1982
10
4300
115
13
4
50
23 Sept 1982

Fig. 4. Distribution of Red-necked Phalaropes at Mono Lake, California, in 1981 and 1982.

ipation of departure. In mid-September 1983, phalaropes foraged mainly at the southwestern and southeastern corners of the lake. In those areas the rising lake had inundated freshwater marshes, creating new substrate for flies in the form of submerged vegetation, and the drowned plants were blackened by masses of pupae.

FOOD.—To study feeding habits, I collected birds in many localities, making deliberate efforts to sample in offshore localities as well as at sites remote from submerged rocks

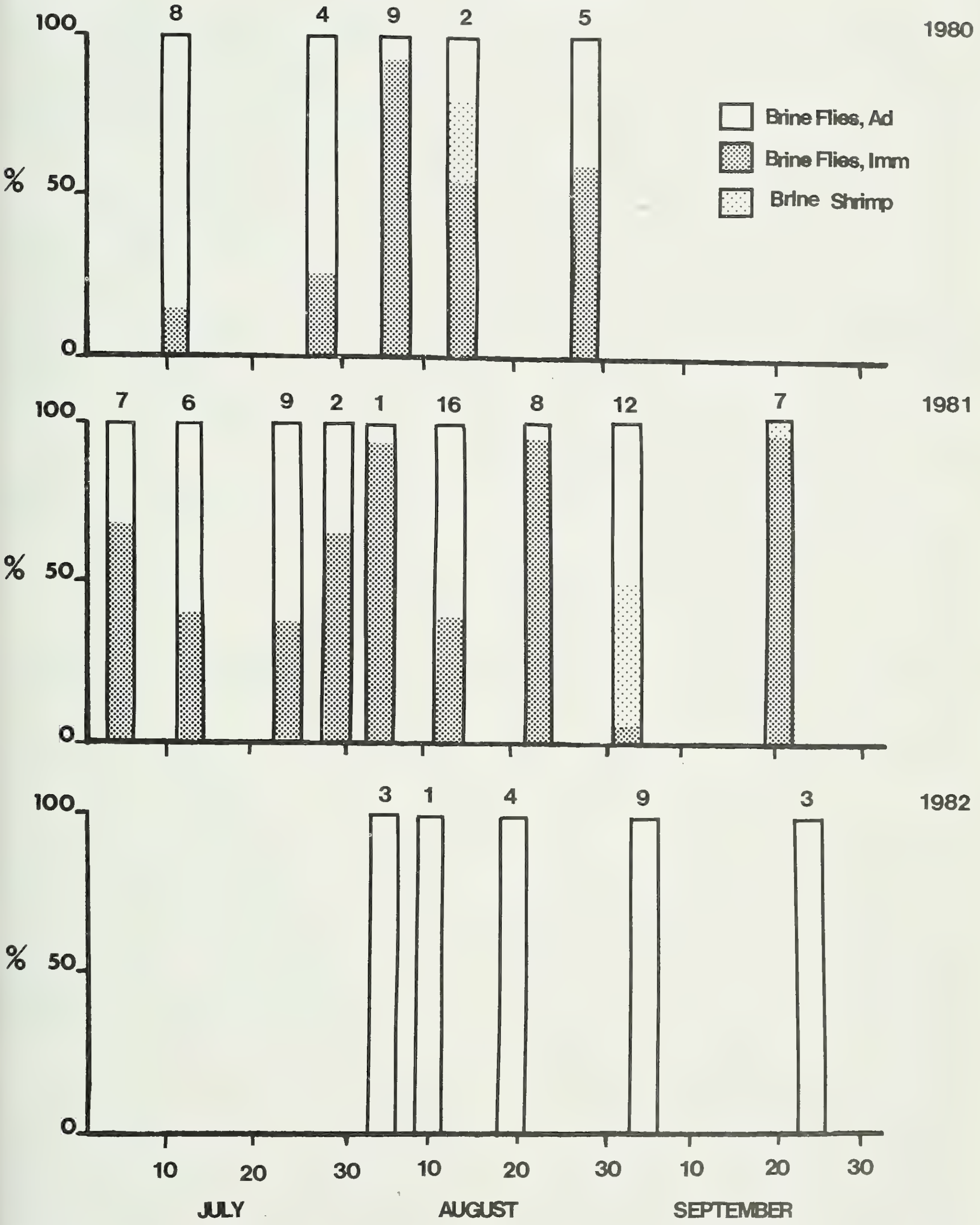

Fig. 5. Diet (% volume) of Red-necked Phalaropes at Mono Lake, California, in 1980, 1981, and 1982. In 1982 the stages of brine flies were not determined after 8 August. Numbers above columns refer to sample size.

Cursory observations of birds feeding over swarms of brine shrimp could easily lead one to infer that shrimp compose the bulk of the phalarope diet. However, careful scrutiny showed that the birds were ignoring shrimp and waiting until an adult brine fly passed by or until water currents wafted a larva or pupa within reach. If this did not occur within five seconds or so, the birds ceased their typical "swim and peck" foraging method and began spinning, which quickly brought larvae to the surface.

Volumetric analysis of stomach contents (Fig. 5) showed that brine flies made up essentially all the diet in July-August, and well over 90% later in the year. The predominance of dipterans was also shown by Wetmore (1925) at Great Salt Lake and by K. Boula (personal communication) at Lake Abert. I estimate that brine flies composed approximately 99% of the phalaropes' diet at Mono Lake. Gravel was present in 70% of the samples, and seeds or unidentified plant parts in 5%. I found no age or sex differences in food preference. Brine fly larvae were the only prey found in the single spring sample (30 April 1984).

In 1980 only 1 adult (14 August) had fed on brine shrimp. In 1981 phalaropes fed exclusively on flies through 21 August. At the next sampling period, 1–2 September, all of 12 birds collected offshore had fed mainly on shrimp, and 7 also contained fly parts; 1 of 7 birds on 21 September contained a few shrimp eggs. In 1982, to investigate the possibility of a seasonal shift in diet, I biased my sampling methods and collected only in offshore sites, and mostly late in the season. Although these samples included birds feeding directly on or over a commercial trap for brine shrimp, no shrimp were encountered. I infer that they are taken mainly when brine flies are unavailable.

WATER USE.—Red-necked Phalaropes visit freshwater sources on the periphery of Mono Lake, often in association with Wilson's Phalaropes (*P. tricolor*), to drink and bathe. Their visitations seem irregular, and daily access to fresh water does not seem to be required. Birds often bathe in the lake itself, sometimes over sublacustrine springs from which fresh water boils to the surface. Formerly, in the 1970s, Red-necked Phalaropes regularly visited small ponds just north of the lakeshore, where many hundreds (M. Morton, personal communication) to several thousand might be seen (Winkler 1977). As the lake has receded, pond use has declined. In 1980 fewer than 500 frequented the ponds each day, in 1981 birds were less abundant, and since 1982 the ponds have been avoided. Visitations occurred mainly in late afternoon, or even after dark, when groups of 5 to 20 might fly in. After circling nervously for several minutes, they would alight and bathe or drink frantically for 30–60 seconds before returning directly to the lake. This nervous behavior was unlike their calm demeanor at freshwater sources on the lakeshore, where they might bathe and preen for an hour or more. Presumably it was related to a greater risk of predation.

WEIGHT.—Weight data are shown in Figure 6. Since Red-necked Phalaropes, unlike many migratory shorebirds, do not lay on great fat stores at this point in their migration, it follows that they do not use Mono Lake as a staging area but only as a stop-over location. Fat-free weights of 6 adult females averaged 29.3 g (range 24.8–32.0) and of 10 males 27.8 g (range 24.2–33.4), which is ca 0.3 g less than the mean arrival weights.

MORPHOMETRICS.—Mensural data are presented in Table 2. Although there is no recognized variation in this species, it may eventually be possible to infer the source of the migrants if mensural data from other areas reveal significant differences.

BEHAVIOR.—Phalaropes make sporadic visits to fresh water and sometimes come ashore or climb on tufa boulders to rest and preen. Otherwise, they remain continuously near feeding areas and fly only short distances each day. It is not uncommon to see a half-dozen feeding over a single pupa-covered rock, pecking larval flies from the water column or lunging at adults as they come to the surface. Occasionally one to two birds will act as satellites to a Wilson's Phalarope, waiting for food that the larger bird spins to the surface (Fig. 7). Whether this commensal activity is an energy-saving device or indicates that the Red-necked Phalarope's effectiveness in spinning is less than that of the larger, longer-legged Wilson's is unknown.

MOLT.—Cramp and Simmons (1983: 639) reported that male Red-necked Phalaropes undergo limited molt on the head and neck on the breeding grounds but that females delay until after the start of migration (see also Hildén and Vuolanto 1972). They also reported that (1) molt began in "moulting areas near the breeding grounds," (2) renewal of flight feathers did not usually commence unti late September, and (3) southward migration began in August or September.

Data from Mono Lake modify those conclusions. Migration begins in July, and the first migrants appearing shortly after their disap-

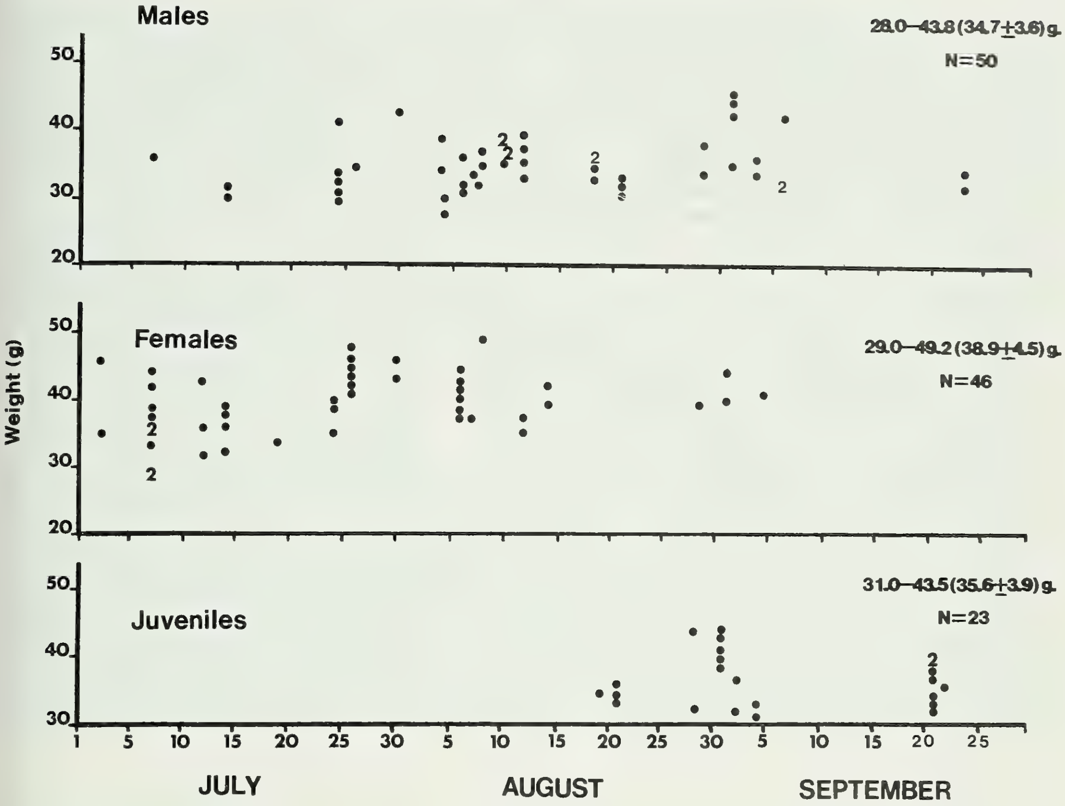

Fig. 6. Weights of Red-necked Phalaropes based on combined samples from 1980 through 1982.

TABLE 2. Measurements (mm) of Red-necked Phalaropes at Mono Lake, California, 1980–1982.

	Exposed culmen		Wing, flat		Tarsus	
	N	Range and mean S.D.	N	Range and mean S.D.	N	Range and mean S.D.
Adult female	47	20.5–24.9 (22.7) ± 1.0	48	105–116 (111.2) ± 2.3	48	19.2–22.2 (20.7) ± 0.7
Adult male	53	20.2–24.8 (22.5) ± 1.0	53	100–113 (106.3) ± 2.9	54	19.4–22.2 (20.9) ± 0.7
Juvenile female	13	22.2–23.5 (22.8) ± 0.4	13	100–114 (108.6) ± 3.7	13	19.4–22.0 (20.9) ± 0.8
Juvenile male	9	20.4–23.0 (21.7) ± 1.0	9	100–109 (103.7) ± 3.3	9	19.5–21.4 (20.3) ± 0.7

pearance from North American breeding areas is noted, (e.g., Jehl and Smith 1970). This schedule allows no time for stops at supposed molting areas.

Adults of either sex begin molting on the nesting grounds, probably at about the same time. From 8 through 12 July 1980, five of eight newly arrived postbreeding females showed light to moderate molt in most of the body tracts, two had just started to molt on the head and neck, and one had not begun. By late July most females showed moderate to heavy molt on the body, and by mid-August many appeared to be in basic plumage, although many feathers had not yet been replaced. The degree of molt in the earliest males, which arrive two weeks later than females, is less than in females examined on the same date. As late as 8 August, however, a few males showed no molt in any tract. Molt of the primaries in each sex (Fig. 8) starts in early August; therefore, many females leave Mono Lake before replacing any. All but one female examined after late August, however, had replaced the inner four or five primaries on each wing. Wing molt in males begins slightly later; one male had not molted any primaries as late as 23 September. I found no evidence

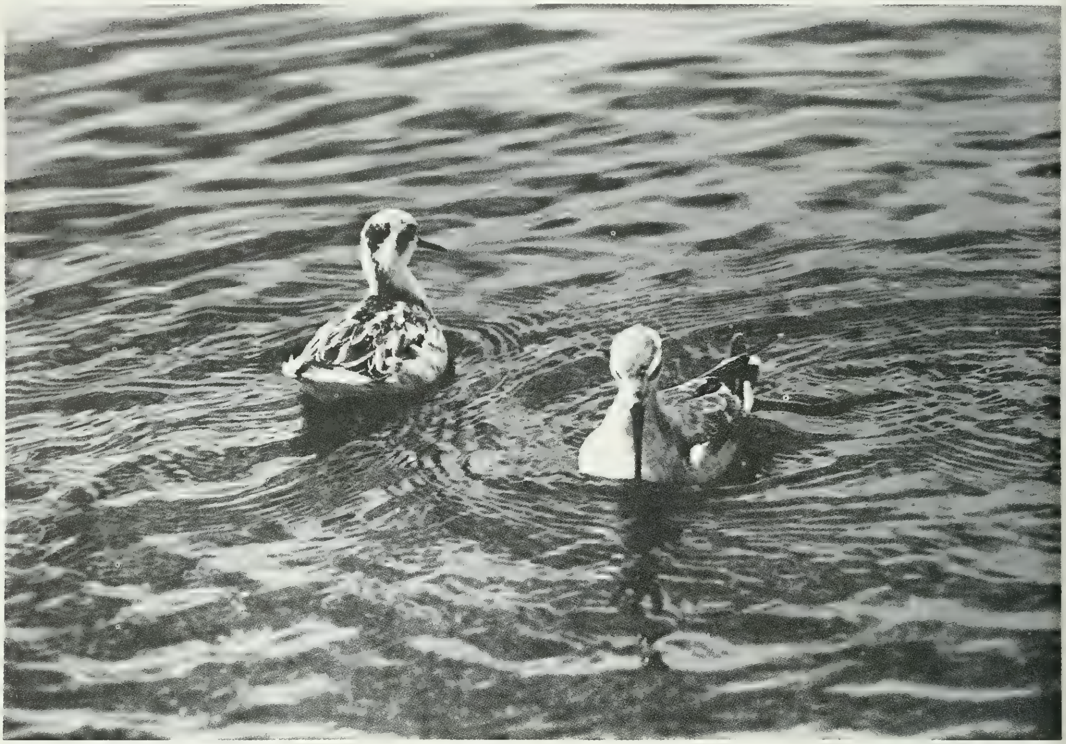

Fig. 7. A Red-necked Phalarope feeding commensally with a Wilson's Phalarope (foreground).

of molt of secondaries or wing coverts, except for the irregular replacement of some greater secondary coverts.

Tail molt (Fig. 9) in many females begins by early July, perhaps while they are still on the nesting grounds. All females examined after late July had molted some rectrices, but only one had completed molt by late August. In males the start of tail molt coincides with their arrival in late July, and all but two examined after 7 August showed some molt. One had replaced all rectrices by 5 September, whereas another on 23 September had not started. The central pair of rectrices is lost first, usually followed by the outer pair or pairs, but this is not invariable and molt is not necessarily symmetrical. One male taken on 28 August had 14 rectrices, of which the central and outer pair were half grown and the fourth pair was just starting to grow.

Juveniles, which arrive in mid-August, have not started to molt body feathers. Some are in heavy molt by late August and nearly all show body molt before departing; one on 21 September, however, had none. Molt of the rectrices may start in late August, but even by late September it remains slight. Juveniles do not replace primaries at this time.

MORTALITY.—I used beached bird censues to index mortality patterns. Although censuses along 8–16 km of shoreline were made at two-week intervals (often more frequently) in several localities and were spread over the entire migration periods of 1981–1984 (irregular surveys were made in 1980 and 1985), I found only two dead phalaropes. Evidently this phase of the migration imposes no great stress on the species.

RED PHALAROPE.—The Red Phalarope (*P. fulicaria*) is rare in the interior of the western states and provinces (Goossen and Busby 1979). The species remains in the Arctic late into the fall, and inland records, as for the Red-necked Phalarope, probably pertain to birds from the western and central Arctic that are en route to wintering areas in the Pacific. At Mono Lake one or two Red Phalaropes have been recorded in four of six years since 1980, all but one of the sightings (1 September 1980) occurring between 14 and 23 October (1981-1, 1982-2, 1983-1). Goossen and Busby (1979) suggested that most fall migrants in the

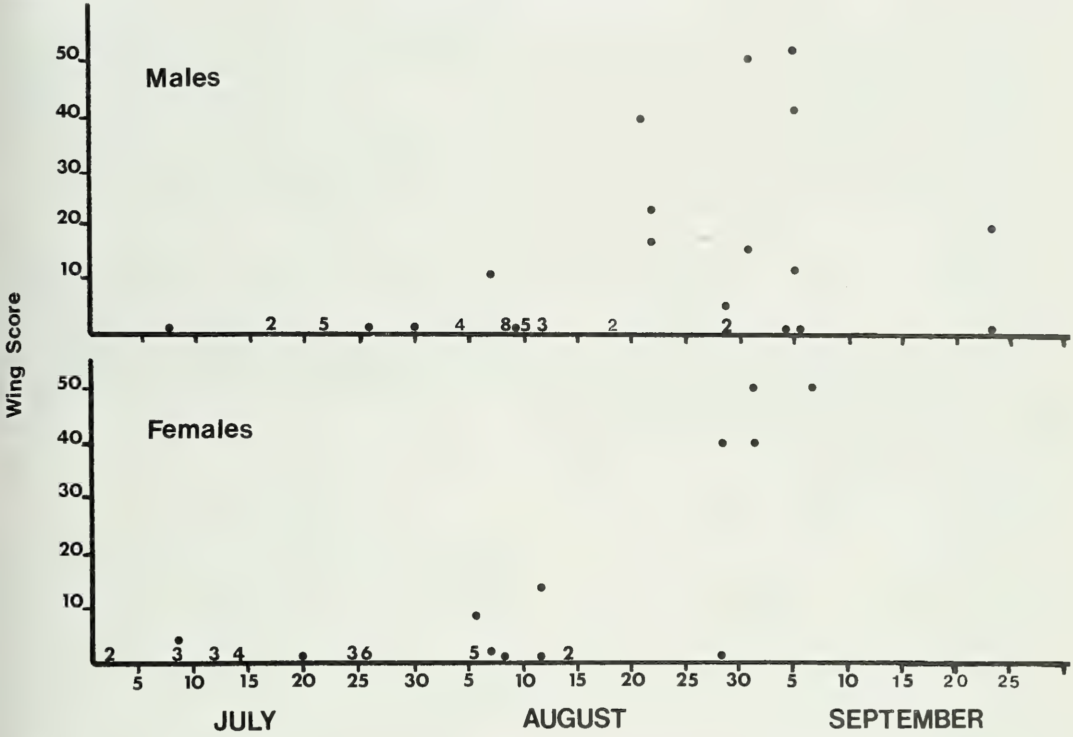

Fig. 8. Wing molt scores of Red-necked Phalaropes based on combined samples from 1980 through 1982.

interior were juveniles. Two of three that I have seen were juveniles; the third was an adult found dead. The juveniles seemed healthy and were feeding well offshore, apparently on brine shrimp.

DISCUSSION

The Red-necked Phalarope uses lakes in the Great Basin as a stopover point on the southward migration and not as a molting or staging area. At Lake Abert, Oregon, K. Boula (personal communication) reported peak numbers of 5,000–7,000 in the first three weeks of August. At Mono Lake I found that peak populations of ca 12,000 were attained by early August and maintained into early September, whereas Winkler (1977) reported the greatest numbers in late August. From shore-based observations, he estimated 21,600 on 30 August 1976, and H. Cogswell (personal communication) estimated more than 40,000 on 22 August 1958. Whether these apparent differences in abundance and timing may pertain to censusing methods, exceptionally large flights in 1958 and 1976, the availability of alternative stopping places in some years, or other factors is unknown. In mid-September 1985, when only a few hundred birds were seen in an incomplete survey of Mono Lake, S. Thompson (personal communication) reported 16,000 near Fallon, Nevada.

Historical data are too scanty to determine if there has been any change in the size of the population using Mono Lake. Fisher (1902) reported "countless hundreds." Grinnell et al. (1918) considered the species very common but barely mentioned Wilson's Phalarope, which currently predominates; perhaps information available to them was inadequate to differentiate between the two species or was based on seasonal data obtained after the main migration of Wilson's Phalarope, which is largely completed by mid-August.

The composition of the Red-necked Phalarope population remained fairly constant during this study. Adult males outnumbered adult females 5:4. This might indicate a faster stopover period for females or their reliance on different migration routes or staging areas, as may be the case for Wilson's Phalarope (Jehl, unpublished manuscript). I suspect, however, that the differences are real

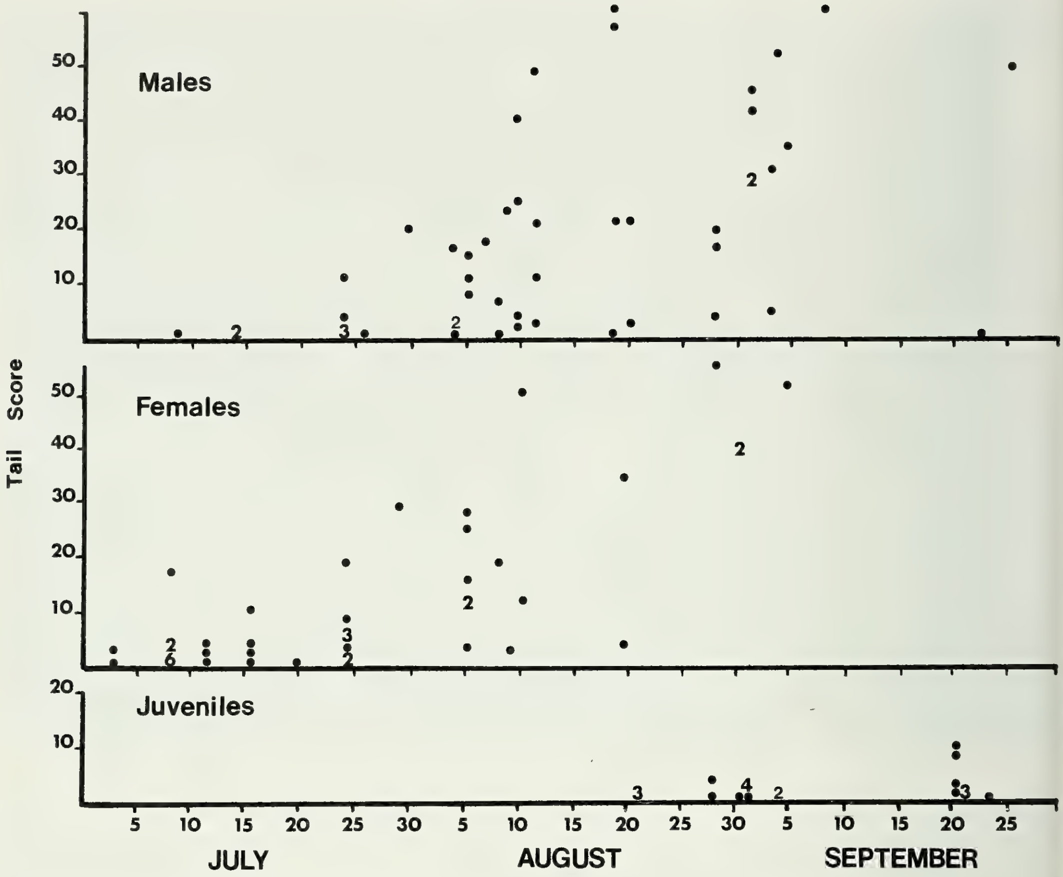

Fig. 9. Tail molt scores of Red-necked Phalaropes based on combined samples from 1980 through 1982.

and indicate an unbalanced tertiary sex ratio, as would be expected in a polyandrous species.

Total population size varied each year from ca 52,000 to 65,000, except in 1983, when it dropped to ca 36,000. The lower numbers in that year cannot be ascribed to censusing error, as techniques and observers remained constant. Nor can they be due to unfavorable food conditions (brine flies were exceptionally abundant) or to a poor breeding season (young were present in expected proportions). Because the migrant population at Lake Abert was judged to be ca 30% below normal (K. Boula, personal communication), I infer that regional events were involved. Two possibilities seem of potential importance. Fresh water was abundant in the far west in 1983, a result of the atypically wet winter of 1982. As a result many aquatic habitats were renewed, and those may have provided alternative stopping points. Perhaps of far greater significance, however, was an apparent drop in breeding populations in the spring of 1983. Low numbers were recorded in the central Canadian Arctic (Churchill, Manitoba, J. Reynolds, personal communication) as well as in the Gulf of Alaska (Middleton Island, P. Gould, personal communication). Birds nesting in those areas presumably winter in the equatorial Pacific off South America, an area that was profoundly affected by an El Niño of unprecedented strength (Rasmusson 1985). The abnormally warm waters are known to have had dramatic effects on breeding birds in the central and eastern Pacific. Reproduction failed at Christmas Island (Schreiber and Schreiber 1984), and in areas influenced by the Humboldt Current major oceanographic changes affected the distribution of fish, seabirds, and marine mammals (Barber and Chavez 1983). I suspect that phalaropes suffered very high mortality on the wintering grounds in 1982, which could not be made up by the production of young in the following breeding season, thus accounting for the low migrant populations of 1983.

Schreiber and Schreiber (1984) noted that "field biologists must recognize that atmospheric circulation patterns that undergo irregular anomalies may affect their study regions and species far from marine ecosystems." Events at Mono Lake illustrate this and point out the difficulties in trying to understand the population dynamics of migratory species in the absence of information about condition and events throughout the range.

ACKNOWLEDGEMENTS

This study was funded by the Los Angeles Department of Water and Power, with a cooperative agreement with the U.S. Fish and Wildlife Service. Additional support was received from Hubbs Marine Research Institute, San Diego State University, National Geographic Society, Kawasaki Motors of America, and Sevylor Boats. Permits were issued by the California Department of Parks and Recreation and Fish and Game, U.S. Fish and Wildlife Service, U.S. Bureau of Land Management, and U.S. Forest Service.

Many persons contributed to this study; D. Babb, K. Boula, S. Bond, B. Cord, H. Cogswell, J. Granito, R. Jarvis, D. Jehl, R. Kastelein, P. Kelly, D. Kent, C. D. Littlefield, S. Mahoney, M. Messersmith, D. Shuford, B. Tillemans, S. Thompson, D. Winkler. Personnel from the Mono Lake Tufa State Reserve helped facilitate the field work. J. Bright and the staff of the Cain Ranch, Lee Vining, California, provided outstanding support at all times.

A draft of the manuscript benefited from the criticism of K. Garrett, S. Hurlbert, A. Pollak, R. Schreiber, and N. K. Johnson.

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SOME RELATIONSHIPS OF BLACK-TAILED PRAIRIE DOGS TO LIVESTOCK GRAZING

Craig J. Knowles[1]

ABSTRACT.—Relationships of black-tailed prairie dogs (*Cynomys ludovicianus*) to livestock grazing were studied from 1973 to 1983 on the Charles M. Russell National Wildlife Refuge and the Fort Belknap Indian Reservation in northeast Montana. A total of 154 prairie dog colony sites was examined, and most were in association with livestock watering sites and/or areas where the topsoil was disturbed by human activity. Roads and cattle trails were found in 150 of the prairie dog colonies. Prairie dog colonies were found to be located significantly ($p < 0.001$) closer to livestock water developments and homestead sites than randomly located points. Observations showed cattle to occur significantly ($p < 0.05$) more on quarter sections with prairie dog colonies as opposed to quarter sections without prairie dog colonies. Forage utilization at one prairie dog colony was estimated at 90% by midsummer. Prairie dogs consumed about a third of the vegetation, with grasses the predominant forage class used.

Habitat characteristics of black-tailed prairie dogs (*Cynomys ludovicianus*) colonies have been reported on over a wide geographic region (Reid 1954, Koford 1958, Smith 1967, Hassien 1976). Prairie dogs are frequently associated with areas of low-growing vegetation and areas intensively grazed by ungulates (Mead 1898, Osborn and Allan 1949, King 1955, Koford 1958, Smith 1967). Although many authors have commented on this relationship, little quantitative information exists on the subject. Furthermore, it is not clear in the literature if prairie dog colonies develop at intensively grazed sites or if the presence of prairie dogs attracts ungulates to an area. There are documented cases of declining prairie dog numbers following reduction or elimination of ungulates from an area (Mead 1898, Osborn and Allen 1949, Uresk and Bjugstad 1983). Knowledge of the spacial distribution and habitat use of ungulates and prairie dogs over a broad area is important to understanding prairie dog-ungulate relationships. The purpose of this study was to investigate the distribution, habitat use, and forage utilization of black-tailed prairie dogs and domestic livestock in northeastern Montana.

STUDY AREA AND METHODS

Data were gathered from 1973 through 1975 and from 1978 through 1980 on the Charles M. Russell National Wildlife Refuge (CMRNWR) and during 1983 on the Fort Belknap Indian Reservation (FBIR) in northeast Montana. The CMRNWR is typified by rough, river breaks country merging with rolling prairies on either side of the Missouri River. Coniferous forest habitats dominated by ponderosa pine (*Pinus ponderosa*) and Rocky Mountain juniper (*Juniperus scopulorum*) are commonly found on the steeper slopes along the Missouri River and cover about 36% of the land area. Shrub-grassland and grassland habitats occur on the broad ridge tops and coulee bottoms that extend from the prairies onto the CMRNWR. Glaciated prairies with relatively little topographic relief compose the majority of the FBIR. Shrub-grassland and grassland habitats dominate these sites. Coniferous habitats occur only on the foothills of the Little Rocky Mountains that border the FBIR on the south.

Prairie dog colonies on both the CMRNWR and the FBIR are restricted to the shrub-grassland and grassland habitats. Western wheatgrass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*), green needlegrass (*Stipa viridula*), and needle-and-thread grass (*S. comata*) are the predominant grasses in these habitats. Common forbs include fringed sagewort (*Artemisia frigida*), plains prickly pear (*Opuntia polycantha*), and yellow sweetclover (*Melilotus officinale*). The shrub layer is composed largely of big and silver sagebrush (*Artemisia tridentata, A. cana*) and greasewood (*Sarcobatus vermiculatus*). The CMRNWR and the FBIR are grazed primarily by cattle, although sheep and horses are present in a few grazing allotments. Native ungulates are pronghorns (*Antilocapra americana*), elk (*Cervus elaphus*), and mule and white-tailed deer (*Odocoileus hemionus, O. virginianus*).

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The CMRNWR was surveyed for prairie dog colony sites in 1979. Colonies were mapped on frosted mylar plastic over 1:24,000 aerial photos while driving or walking the perimeter of the colony. The area of each colony was determined with an electronic digitizer. Prairie dog colonies on the FBIR (survey area boundaries described in Knowles and Knowles 1984) were surveyed in 1983 and were mapped on 7.5′ USGS topographic maps. Area for each colony was determined with a dot grid. At each prairie dog colony site, I recorded presence or absence of prairie dogs, livestock developments (reservoirs, wells, salt licks, and calf feeders), homesteading activity, roads, and well-established cattle trails. Complete survey coverage was made of each study area. However, on FBIR inactive colony sites were not investigated nor was one small colony located around a private residence.

Special effort was made to study prairie dogs at the west end of the CMRNWR north of the Missouri River because of the number (36) and density (6.3 colonies/100 km^2) of prairie dog colonies. All stock water developments and homestead sites were accurately located on a map over a 570 km^2 area. I used a Students t-test to test the hypothesis that mean distance from the geographic center of each prairie dog colony in this area to the nearest stock water development or homestead site was not different than the mean distance to such features for 120 randomly chosen points. In this same area, I made weekly surveys of cattle each summer and fall from 1973 to 1975 in two pastures (20,244 ha) of the four-pasture Nichols Coulee rest-rotation grazing system as part of another study (Knowles and Campbell 1982). Quarter section location, habitat type, and slope were recorded for each cattle group when first observed. The quarter section distribution of cattle was compared to the quarter section distribution of prairie dog colonies occurring in these two pastures using a chi-square test of homogeneity. Habitat type designation followed Mackie (1970) except for analysis purposes, where observations of cattle in the *Xanthium strumarium* and *Agropyron-Symphoricarpos* habitat types were combined and observations in the *Artemisia longifolia* and *Pinus-Juniperus* habitat types were combined.

Spring/summer forage utilization of prairie dogs, prairie dogs and other wildlife (primarily mule deer and elk), and prairie dogs and cattle was investigated at a prairie dog colony located next to a reservoir site in the Nichols Coulee allotment. A 7.7 ha area of the 16.4 ha colony was fenced to exclude cattle in July 1978. Ten agronomy cages were placed on each side of the fence that passed through the center of the colony in pairs at 5 m intervals. The 10 cages within the exclosure had a mesh of 25 × 50 mm, and the other 10 cages had a mesh size of 51 × 76 mm. The larger mesh allowed prairie dogs to enter the cages. The cages were placed on the site in November 1979 (pasture rested in 1979), and in early August 1980 a 1.2 m^2 area was sampled in each cage. In addition, 10, 1.2 m^2 areas were sampled on either side of the exclosure fence midway between each agronomy cage. Forbs and grasses were bagged separately, oven dried, and weighed to the nearest gram. A Kruskal-Wallis one-way analysis of variance was used to statistically test for differences among grazing regimes.

RESULTS

A total of 112 prairie dog colony sites was found on the CMRNWR (Table 1). Ninety-six of these colonies were active, occupying a total of 2,122 ha and averaging 22 ha in size (se ± 47 ha, range < 1 – 307 ha). Approximately 0.6% of the land area was inhabited by prairie dogs, with 2.8 active prairie dog colonies per 100 km^2. On the FBIR, 42 active prairie dog colonies were surveyed totaling 2,786 ha ($\bar{x}$ = 66 ha, se ± 91 ha, range 3 – 372 ha). Prairie dogs occupied about 2.1% of the survey area on the FBIR, with 3.0 colonies per 100 km^2.

The majority of prairie dog colonies both on the CMRNWR and FBIR were located in ar-

TABLE 1. Distribution of prairie dog colonies found in association with livestock developments, natural bodies of water, homesteads, and roads and cattle trails.

		Percentage of colony sites located next to			
Study area	n	Livestock developments	Streams & lakes	Homesteads	Trails & roads
CMRNWR[1]	112	62	18	26	97
FBIR[2]	42	60	29	17	98

[1] Charles M. Russell National Wildlife Refuge.

[2] Fort Belknap Indian Reservation.

eas of intensive livestock grazing and/or areas of topsoil disturbance by human activity. Livestock developments (reservoirs, wells, salt licks, and calf feeders) were found at 62% of the colony sites on the CMRNWR and 60% of the colony sites on the FBIR (Table 1). Nine colonies on the CMRNWR had salt licks or calf feeders in them; four of these colonies were located away from a stock watering area. Many colonies at the east end of the CMRNWR were adjacent to the waters of Fort Peck Reservoir. On the FBIR, 29% of the colonies were found along perennial streams or around dry lakes. These sites were areas of intensive livestock grazing on both study areas.

Homestead activity was found at 26% and 17% of the colony sites on the CMRNWR and FBIR, respectively. Stock watering areas and areas formerly cultivated were frequently found at homestead sites. Only one small colony (< 1 ha) was found in a grain field currently under cultivation. Included in this group is a prairie dog colony on the CMRNWR that started at a site where gravel was removed for road construction and another that started on a greasewood bottomland site that was mechanically cleared and leveled to make a pasture for horses at a refuge field station. Roads (usually two-track vehicle trails) and/or well-established cattle trails were found at 109 of the 112 prairie dog colony sites on the CMRNWR and at 41 of 42 colonies on the FBIR. Roads alone intersected 88% of the prairie dog colonies on the CMRNWR. Roads and cattle trails on both the CMRNWR and the FBIR interconnected livestock watering areas and homestead sites.

In the northwest portion of the CMRNWR, the mean distance from the geographic center of 36 prairie dog colony sites to the nearest stock water development or homestead site (0.5 km) was less than ($p < 0.001$, $t=1084.36$, 154 d.f.) the mean (1.3 km) for the 120 random points. Thirty of the 81 stock water developments in this area had colonies at them. The quarter section locations of 1,772 observations of cattle groups recorded from 1973 to 1975 in the Nichols Coulee allotment were not distributed homogeneously with respect to quarter sections with prairie dog colonies ($p < 0.05$ $X^2=4.90$, 1 d.f.). Cattle were observed with greater than expected frequency on quarter sections with prairie dog colonies. However, the distribution of cattle observations on quarter sections with reservoir sites lacking prairie dog colonies was homogeneous to the distribution of cattle observations on quarter sections with prairie dog colonies ($0.50 < p < 0.75$, $X^2=0.16$, 1 d.f.), suggesting that the concentration of cattle on quarter sections with colonies is related primarily to a source of water.

Cattle were observed to primarily use the *Artemisia-Agropyron* and *Sarcobatus-Agropyron* habitat types during both summer and fall (Table 2). Use of shrub-grassland habitats averaged 85% over both seasons for all years. These habitats, as determined from aerial photos, composed only 54% of the two pastures. More than three-fourths of the observations of cattle were on slopes with inclinations of less than 11 degrees. Cattle, for the most part, restricted their use to the shrub-grassland habitats along the main ridge tops and major drainages where water developments (reservoirs and wells) had been established. All prairie dog colonies in these two pastures were located in shrub-grassland habitat types (*Artemisia-Agropyron*, 88%; *Sarcobatus-Agropyron*, 12%). Without exception, these colonies were located primarily on slopes of less than 7 degrees. Prairie dog colonies occupied 2.8% of these two pastures, which was considerably above the average for the CMRNWR. Number of colonies per 100 km^2 (8.9)

TABLE 2. Use of habitat type and slope by cattle during summer and fall in the Nichols Coulee allotment.

	Percentage of observations	
Habitat type	Summer	Fall
Artemisia-Agropyron	44	42
Sarcobatus-Agropyron	29	27
Agropyron-Symphoricarpos	13	15
Pinus-Juniperus	14	16
Degrees of slope		
0–10	81	79
11–25	14	13
26–35	5	7
36+	<1	1

in these two pastures was also above the average for the CMRNWR.

Total plant production along the utilization transect averaged 867 kg/ha (Table 3). Plant biomass for each plant category varied significantly among grazing regimes (total plants $p < 0.01$, $H = 12.18$, 3 d.f., grass $p < 0.005$, $H = 15.78$, 3 d.f., forbs $p < 0.05$, $H = 7.91$, 3 d.f.) (Table 3). Utilization by prairie dogs was estimated at 29%, by prairie dogs and other wildlife at 56%, and by prairie dogs, other wildlife, and cattle at 90%. Observations throughout the summer indicated that elk were the primary wildlife species to graze on the prairie dog colony, and most of this activity was confined to the exclosure. Utilization by prairie dogs was directed largely at grasses, whereas utilization was more evenly distributed among grasses and forbs when prairie dogs grazed in conjunction with other ungulates.

DISCUSSION

Prairie dogs on the CMRNWR and the FBIR were associated with areas intensively grazed by livestock and/or areas where the topsoil had been disturbed by human activity. The association of prairie dog colonies with intensive grazing by ungulates, with rangelands in poor condition, with stock watering sites, or with homestead sites, has been noted by others (Mead 1898, Osborn and Allen 1949, Reid 1954, King 1955, Koford 1958, Smith 1967, Hassien 1976, Hillman et al. 1978, and Dalsted et al. 1981, Uresk and Bjugstad 1983). On the CMRNWR I was able to establish that prairie dog colonies appeared after the disturbance in five instances. In addition, conversations with local ranchers indicated that the prairie dog colonies at stock reservoirs came after construction of the reservoirs. Moreover, it is doubtful that homesteads were purposely located in a prairie dog colony. Based on these observations, it appears that in my study areas prairie dog colonization at stock watering sites and homesteads followed the intensive grazing and soil disturbance.

At least four factors may be important in explaining this high association of prairie dog colonies with intensively grazed sites. (1) In the Nichols Coulee allotment, the habitat types and topographic situations most used by cattle were also sites most suitable for prairie dog colonization. (2) Roads and trails appear to facilitate prairie dog dispersal (Koford 1958, Knowles 1985). Dispersing prairie dogs following roads and trails have an increased chance of finding disturbed sites because roads and trails on both study areas interconnected livestock developments and homesteads. The high occurrence of roads and trails in prairie dog colonies has not been previously reported. However, I found roads or trails through prairie dog colonies of study area maps for Anthony and Foreman (1951), Reid (1954), Klatt (1971), Stockrahm (1979), and Coppock (1981). (3) Extracolony dispersing prairie dogs are at least a year old upon dispersal (Garrett 1982, Knowles 1985) and may actually recognize and select for heavily grazed areas (Uresk and Bjugstad 1983). (4) Predation mortality of colonizing prairie dogs at grazed sites may be lower than at ungrazed sites. Although this explanation seems plausible, there is little factual information supporting it, and more research on prairie dog dispersal and predation is needed.

Although cattle appeared to selectively use quarter sections with prairie dog colonies in the two pastures of the Nichols Coulee allotment, it may have been related to a source of water in most colonies. Hassien (1976) found significantly greater numbers of cattle droppings in prairie dog colonies than adjacent areas. Greater use of prairie dog colonies may also be attributed to increased abundance of forbs (Osborn and Allan 1949, King 1955, Koford 1958, Hassien 1976, Coppock 1981, O'Meilia et al. 1982, Knowles et al. 1982), increased vegetative production (Uresk and

TABLE 3. Comparison of total plant, grass, and forb biomass under different grazing regimes at a prairie dog colony in the Nichols Coulee allotment.

	Biomass kg/ha (% utilization)		
Grazing category	Total plant[1]	Grass[1]	Forbs[1]
Ungrazed	867	364	503
Prairie dogs	613 (29)	135 (63)	478 (5)
Prairie dogs/wildlife	379 (56)	138 (62)	241 (52)
Prairie dogs/cattle	85 (90)	24 (93)	61 (88)

[1] Kruskal-Wallis 1-way ANOVA, significant ($p < 0.05$) difference among grazing categories.

Bjugstad 1983), increased soil nutrients (Hassien 1976), and greater nitrogen concentration in plants (Coppock 1981) in prairie dog colonies.

The relatively greater abundance of prairie dogs in the Nichols Coulee allotment when compared to the rest of the CMRNWR was probably related to a greater availability of prime habitat for prairie dogs in this area. However, construction of numerous reservoirs and wells in association with implementation of the rest-rotation grazing system in the mid-1960s undoubtedly played a role in the establishment of prairie dog colonies in this grazing system. It is also possible that the early turn-in date (1 April) and intensive, early grazing associated with two pasture treatments facilitated pioneering prairie dogs in establishing colonies.

Forage utilization in the unrestricted portion of the utilization transect (90%) was already excessive by midsummer. Cattle were only present in this pasture from 1 April through 31 July. O'Meilia et al. (1982) found forage utilization in his prairie dog–cattle pastures to be 95% and 96%, whereas in cattle-only pastures it was 80% and 92%. They estimated use by prairie dogs to range from 33% to 37% through September under a density of prairie dogs (21 to 30/ha) very similar to that which I observed in my study colony (9 to 31/ha, Knowles 1982). Hansen and Gold (1977) estimated total reduction in vegetation because of prairie dogs at 18%; basing this figure on density of prairie dogs at their study site (7.3/ha), food requirements, and denuded area of mounds. The selection of grasses by prairie dogs at this colony is consistent with recent prairie dog food habits studies (Summers and Linder 1978, Fagerstone et al. 1981, Wydeven and Dahlgren 1982, Uresk 1984).

ACKNOWLEDGMENTS

The following people provided field assistance during this study: S. Gieb, R. Gumtow, A. Hetrick, P. Knowles, S. Schmidt, D. Schuster, and C. Stoner. Drs. B. O'Gara and R. Mackie provided technical advice and guidance through various stages of this study. Others providing assistance were R. Campbell and Drs. M. Behan, T. Clark, R. Hutto, L. Metzgar, A. Sheldon, and P. Wright. I received financial support during various stages of this study from the Montana Department of Fish, Wildlife and Parks, U.S. Fish and Wildlife Service, and the Fort Belknap Community Council.

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EFFECT OF EXCLUDING SHREDDERS ON LEAF LITTER DECOMPOSITION IN TWO STREAMS

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Abstract.—The effect of excluding shredders on leaf processing rates was studied in a Rocky Mountain stream in Utah and a cold desert stream in Washington. Experimentally excluding shredders significantly decreased the processing rate in both streams. Processing rates (k) were higher in the desert stream, and it is postulated that this is related to increased microbial activity due to the higher water temperatures.

The decomposition of allochthonous detritus in stream ecosystems has been shown to be a function of both physical, i.e., temperature and current, and biological, i.e., microbial and macroinvertebrate feeding, effects (Anderson and Sedell 1979). Macroinvertebrate shredders (Merritt and Cummins 1978), which feed directly on leaf litter in streams, have been estimated to account for 20% of total leaf decomposition (Cummins et al. 1973, Petersen and Cummins 1974, Cummins and Klug 1979). Although their role is still imperfectly understood, it is clear that coarse particle detritivores, or shredders, are extremely important members of some stream ecosystems. In the process of shredding leaves, they not only provide themselves with nutrients but convert coarse particulate organic matter (CPOM) to fine particulate organic matter (FPOM) and thus provide an energy source for fine particulate detritivores, or collectors (Cummins et al. 1973, Mackay and Kalff 1973, Cummins 1974, Iversen and Madsen 1977, Short and Maslin 1977, Cummins and Klug 1979). On the other hand, they may have an effect on species that use leaf packs as habitat or graze periphyton from the leaf surface.

The purpose of this paper is to document the importance of large shredders in the decomposition of leaves in two streams, a Rocky Mountain stream and a cold desert stream.

Study Sites

Stewart's Creek is a small second order (Strahler 1957) stream originating from a glacial cirque on Mt. Timpanogos about 33 km northeast of Provo, Utah County, Utah. The mean annual discharge is 0.25 m^3/s, and the annual water temperature ranges from 2.0 to 9.0 C. The stream gradient in the study section is 7%. Riparian vegetation in the study area consists of willow (*Salix* sp.), quaking aspen (*Populus tremuloides*), and box elder (*Acer negundo*). For a more detailed description of the stream, see Sakaguchi (1978) and Oberndorfer et al. (1984).

Rattlesnake Springs is a first order, permanent, spring-fed stream about 43 km northwest of Richland, Benton County, Washington. It originates as seeps and is fed by one major spring, resulting in a base flow of ca 0.01 m^3/s. Mean annual precipitation in the region is ca 14 cm, and the stream water temperature varies bewteen 2.0 and 22.0 C. Rattlesnake Springs is in the shrub-steppe desert in the northerly extension of the cold-desert physiographic province. For further information, see Cushing et al. (1980), Cushing and Wol (1982, 1984).

Methods

Stewart's Creek.—In the fall of 1978, 120 leaf packs were constructed using three grams (dry wt) of box elder leaves. The packs were fastened to lids of one-pint plastic freezer containers as described in Merritt et al. (1979) The freezer containers had all four sides and bottoms cut out. Half (60) of the containers were left open on all sides (control), and hal were covered with 1 mm Nitex (shredder exclusion). For a complete description of the

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TABLE 1. The effect of excluding shredders on (A) mean percent of original leaf material remaining and the rate of decomposition (k) of leaf material in Stewart's Creek, Utah, and (B) the number of shredders, total organisms, and collectors per gram DW leaf material. Numbers are treatment means; means connected by solid line are not significantly different at $\alpha = 0.05$. SX = shredder exclusion, C = control.

A.

	Percent of leaf material remaining						
	Week						
Treatment	0	4	8	12	16	20	k
Shredder exclusion (fine mesh)	100	64	42	18	16	10	−0.0166
Control	100	53	18	6	5	4	−0.0269

B.

Dependent variable		
Shredders	93 (SX)	88 (C)
Total organisms	1139 (C)	430 (SX)
Collectors	1030 (C)	330 (SX)

cages, see Merritt et al. (1979). Leaf packs were randomly assigned to an experimental treatment, placed in the containers, and randomly assigned to transects in the stream. Each treatment was represented in each transect, although the position of the treatment within the transect was determined randomly. The cages were placed over the packs at the beginning of the experiment. Two packs from each of the treatments were removed from the stream according to the following schedule: two packs per treatment per week for two consecutive weeks and four packs per treatment on the third week, for a total of 21 weeks. Four packs were removed every three weeks to give a better estimate of invertebrate numbers. The packs were brought back to the laboratory, where the macroinvertebrates were washed from the leaves. Leaves were dried at 50 C for 48 hr and weighed. Macroinvertebrates were preserved in 70% ethanol and later sorted to lowest taxon possible and counted. The interoccular distance of all *Zapada cinctipes* (Plecoptera: Nemouridae) were measured to determine size distributions. The dates for this experiment were from 14 November 1977 to 7 February 1978.

RATTLESNAKE SPRINGS.—Methods used on Rattlesnake Springs were identical to those described above except that 27 exclusion and 27 control leaf packs were used. This experiment ran for nine weeks, with three leaf packs per treatment removed weekly. No cages were placed over the control packs. The dates for this experiment were from 2 August 1978 to 9 October 1978.

METHODS OF ANALYSIS.—A negative exponential model was used to describe leaf pack processing (e.g., Petersen and Cummins 1974). The effects of treatments on the processing rate coefficients (k) were analyzed, with analysis of covariance using linear contrasts to test for homogeneity of slopes (Hanson 1978).

RESULTS AND DISCUSSION

STEWART'S CREEK, UTAH.—The effects of the experimental treatments on the rates of leaf litter processing are shown in Table 1A. The shredder exclusion treatment (fine mesh) had more leaf material remaining on all dates of the study than the control treatment. There was significant difference ($p < 0.001$) between the shredder exclusion treatment ($k = -0.0166$) and the rates of the control ($k = -0.0269$).

The fine meshed cages (shredder exclusion) were designed and constructed to exclude the larger instars of the dominant shredder, *Zapada cinctipes*, from leaf packs. Smaller *Z. cinctipes* instars were able to pass through the 1 mm mesh screen and colonize the leaf packs within the exclusion cages. Although the control and the shredder exclusion packs had significantly different processing rates, they did not differ in the number of shredders (*Z. cinctipes*) per gram dry weight of leaf material when averaged over the entire sampling period, although the effect of absolute numbers was not tested. The difference in processing rates was probably due to the fact that only smaller *Zapada* were allowed in the exclusion cages, whereas all sizes were found in the control cages. It would appear from these data that not only is the number of shredders im-

TABLE 2. The effect of excluding shredders on (A) mean percent of original leaf material remaining and the rate of decomposition (k) of leaf material in Rattlesnake Springs, Washington, and (B) the number of shredders and total organisms per gram DW leaf material. Numbers are treatment means; means connected by solid line are not significantly different at $\alpha = 0.05$. SX = shredder exclusion, C = control.

A. Percent of leaf material remaining

Treatment	Week 0	2	4	6	8	k
Shredder exclusion (fine mesh)	100	65	41	25	16	−0.0213
Control	100	48	23	12	6	−0.0417

B.

Dependent variable		
Shredders	2.5 (SX)	4.8 (C)
Total organisms	77 (SX)	145 (C)

portant in determining the processing rate but that the size of the shredder is also an important factor to consider. There was a difference between the leaf weight loss rate in the controls and the shredder exclusion treatments, especially between weeks 4 and 8, although there was no difference in the number of shredders (Table 1B).

The dominant functional feeding group in all treatments was the collector-gatherer group (Table 1B). There were significantly fewer collector-gatherers in the shredder exclusion treatment. This was probably due to the exclusionary function of the fine mesh used on the cages in this treatment and/or a response to reduced shredding in the early portion of the experiment.

RATTLESNAKE SPRINGS, WASHINGTON.—Exclusion of shredders in the leaf packs of the cold desert stream results in a significantly lower processing rate (Table 2A). Both the k value for the control packs (k = −0.0417) and the experimental packs (k = −0.213) were higher than their counterparts in Stewart's Creek. Since the major shredders in Rattlesnake Springs were amphipods and essentially excluded from the exclusion packs, it is believed that the higher k rates in the cold desert stream were probably due to increased microbial processing (Reice and Herbst 1982). Short et al. (1984) found higher processing rates of *Salix nigra* leaves in the warmer of two Texas streams, and Suberkropp et al. (1975) and Kaushik and Hynes (1968) documented the positive relation between increased rates of leaf decomposition and increased water temperatures. The water temperature in Rattlesnake Springs during the experiments was 20–22 C. At these temperatures we would expect microbial processing to dominate the system.

Approximately 50% of the control leaf material was processed during each two-week period (Table 2A). There was no significant difference between either the number of shredders per gram dry weight leaf material or the total number of organisms in the control and experimental packs (Table 2B).

CONCLUSIONS

The processing of leaf litter is mediated by ar array of biological and physical factors. By ex cluding shredders in a Rocky Mountain and col desert stream, significantly faster processin rates were found in the leaf packs exposed t shredder processing. Furthermore, the process ing rates in both control and exclusion packs i the cold desert stream were higher than thei counterparts in the Rocky Mountain stream. W attribute this partly to the type of shredder present in the desert stream but more likely t the higher mean water temperature during th experimental period, which probably increase microbial processing.

ACKNOWLEDGMENTS

The research on Stewart's Creek was sup ported by Brigham Young University. Researc performed at Rattlesnake Springs was funded b the U.S. Department of Energy under Contrac DE-AC06-76RLO. Manuscript preparation wa funded under contract DE-AC09-76SROO-81 between the Department of Energy and Univer sity of Georgia Institute of Ecology.

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THREE-YEAR SURVEILLANCE FOR CESTODE INFECTIONS IN SHEEP DOGS IN CENTRAL UTAH[1]

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ABSTRACT.—During the summers of 1982, 1983, and 1984, 269 sheep dogs from an area endemic for hydatid disease were examined for cestodes (*Echinococcus granulosus* and *Taenia* spp.). Each dog was given an oral purge of arecoline hydrobromide and then following purgation received a subcutaneous injection of praziquantel (Droncit®). During the three-year study period, 205 dogs were examined one time only, 48 dogs were examined two of the three years, and 16 dogs were examined each of the three years (= 349 separate examinations). In 1982, 45 of 91 dogs examined (49.5%) harbored at least one species of cestode. Those data for 1983 and 1984 were 55 positive of 141 examined (39.0%) and 34 positive of 117 examined (29.1%), respectively. The marked drop in dogs infected during the second and third year of the study suggests that many sheep ranchers were implementing some of the control measures recommended for prevention of *E. granulosus* infections.

The numbers of separate purgations showing specific cestodes detected in all positive dogs (some dogs naturally with more than one species of cestode) were: *E. granulosus*, 16 (4.6%); *T. hydatigena*, 34 (9.7%); *T. ovis krabbei*, 46 (13.2%); *T. pisiformis*, 47 (13.5%); and *T. serialis*, 24 (6.9%).

As part of an over-all program designed to prevent and/or control the spread of hydatid disease in Utah and neighboring states (Andersen et al. 1983), a three-year surveillance study was planned to determine the prevalence of cestode infections in sheep dogs examined at the summer mountain grazing ranges in Sanpete County. Results of previous surveys had shown that the prevalence of *Echinococcus granulosus* tapeworms (the causative organism of hydatid disease in this region) fluctuated markedly, depending upon whether the majority of dogs examined in any one year were non-sheep dogs from rural communities or were dogs owned by sheepmen and used generally or exclusively in the sheep industry (Andersen et al. 1983). Many epidemiological determinants have been identified as important factors in the distribution and prevalence of *E. granulosus* in Utah, such as the use of local herders, the existence of community herds, the association of sheepmen from several counties on adjacent winter rangelands, and specific sheep-marketing practices (Crellin et al. 1982). Nevertheless, the role of the sheep dog as the principal definitive host of *E. granulosus* in this region remains as the single most important parameter for surveillance evaluation. The majority of sheep herds within Utah are located in Sanpete County, and almost all the surgical cases for removal of hydatid cysts have been people residing in that particular locality o the state (Crellin et al. 1982).

MATERIALS AND METHODS

The specific study area (Sanpete County involved in this project and its unique characteristics that make that region highly suitabl as an endemic site for hydatid disease hav been described earlier by Andersen et al (1983). The majority of summer grazing site are located along or adjacent to the Skylin Drive, a dirt road that traverses north to sout along the summit of the Manti–La Sal mountain range in that county. The mountain reach 3,600 m in elevation, are heavily vegetated with lush growths of forbs and grasses and afford numerous expanses for summe grazing of sheep. The general area is accessible mainly by the road along the summit, bu it is intersected approximately every 10–2 km by roads ascending through canyons tha

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[1] This project was supported in part by U.S. Public Health Service Grant AI-10588; by funds allocated from the College of Biology and Agriculture, Brigha Young University; and from the Division of Community Health Services, Utah Department of Health.

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TABLE 1. Number of sheep dogs examined for cestodes in central Utah, 1982–1984.

		Years		
Examinations		1982	1983	1984
One examination (N = 205)		56	83	66
Two examinations (N = 48)		13 →	repeat	
			29 →	repeat
		6 →	→	repeat
Three examinations (N = 16)		16 →	repeat →	repeat
Total separate dogs = 269	Total examinations per year	= 91	141	117
		Total examinations = 349		

TABLE 2. Prevalence of cestode infections in sheep dogs examined, 1982–1984.

		Positive	Negative
Year	Total examinations	No. (%)	No. (%)
1982	91	45 (49.5)	46 (50.5)
1983	141	55 (39.0)	86 (61.0)
1984	117	34 (29.1)	83 (70.9)
Total	349	134 (38.4)	215 (61.6)

connect to the communities on the valley floor, either to the west or east of the summit. Range sheep herds are routinely grazed in this mountain region during the summer months of May to October and then on the desert (100–200 km to the west) during the winter months (Crellin et al. 1982).

To contact as many sheep ranchers in the region as possible, a listing of all those having summer range allocations in the area specified was secured from the Utah Woolgrowers organization in Salt Lake City, Utah. Each owner was then sent a letter detailing the nature and intent of the project and some basic information on hydatid disease, with an emphasis on the role of sheep and sheep dogs in the life cycle of the causative parasite. All owners were encouraged to make necessary plans and arrangements to have their dogs examined and were informed that all examinations and all subsequent treatment of dogs would be done under the direction of licensed, practicing veterinarians. Furthermore, all services would be free. If anyone had any questions concerning the study, they were instructed to contact their own veterinarian or private physician for additional clarification.

Owing to the mountainous terrain where the grazing sites were located and because of unpredictable time restraints, no schedule could be prearranged when the examining team would be at a specific camp site. Nevertheless, in most cases owners were contacted at least one day in advance to encourage them to allow ample time for the clinic and to fast their dog for approximately 12 hr prior to the actual examination. Such a practice allowed for an evacuation of most of the dog's intestinal contents and made the subsequent purgation less severe.

At the time of the examination, the attendant veterinarian gave educational brochures to each owner and explained the process to be undertaken. Because approximately 10% of all dogs purged and examined at clinics in Utah over the past 12 years have shown some adverse reactions (spasms, labored breathing, incoordination, accelerated heartbeat, etc.), and since many of the highly trained sheep dogs were considered of relatively high monetary value, a release of responsibility form was signed by each owner before his dog could be examined. Also, a questionnaire was filled out identifying the owner's name and address, the number of sheep in each herd, and the name, breed, sex, and age of each dog to be examined. Each owner and each dog were given identification numbers to be used in all subsequent identifications and statistical tabulations.

Each dog was individually tethered with a collar choke chain and given an oral dose of 1.5% arecoline hydrobromide (3 mg/kg of body weight) to induce purging. One or two additional doses were given if no response occurred within an approximate 20–30

Table 3. Prevalence of specific cestodes in sheep dogs examined, 1982–1984.

	Neg.	*E. g.*	*T. h.*	*T.o.k.*	*T. p.*	*T. s.*
Year	No. (%)	No. (%)	No. (%)	No. (%)	No. (%)	No. (%)
1982 (N = 91)	46 (50.5)	10 (11.0)	15 (16.5)	13 (14.3)	22 (24.2)	5 (5.5)
1983 (N = 141)	86 (61.0)	3 (2.1)	8 (5.7)	21 (14.9)	17 (12.1)	13 (9.2)
1984 (N = 117)	83 (70.9)	3 (2.6)	11 (9.4)	12 (10.2)	8 (6.8)	6 (5.1)
Total (N = 349)	215 (61.6)	16 (4.6)	34 (9.7)	46 (13.2)	47 (13.5)	24 (6.9)

Legend:
Neg. = negative
E.g. = *Echinococcus granulosus*
T.h. = *Taenia hydatigena*
T.o.k. = *Taenia ovis krabbei*
T.p. = *Taenia pisiformis*
T.s. = *Taenia serialis*

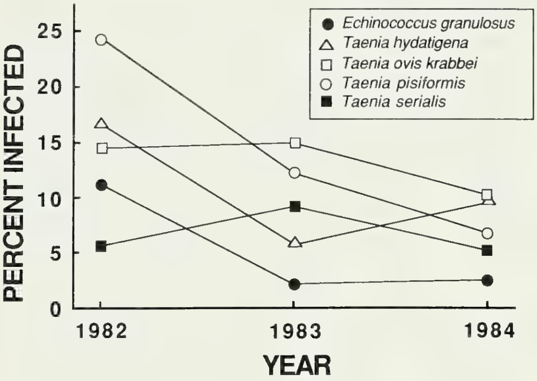

Fig. 1. Prevalence of cestodes in sheep dogs from central Utah, 1982–1984.

minute period following the initial dose. After a purge occurred, any large tapeworms present were carefully collected from the ground and placed into bottles containing 10% formalin. Also, any clear mucoid portion of the purge that might contain the small *E. granulosus* tapeworms was carefully placed in the same bottle, which was then labeled with all pertinent information and stored for laboratory examination. After purgation, each dog was given a subcutaneous injection of praziquantel (Droncit®; 5 mg/kg of body weight), a drug known to be highly effective in the removal of *E. granulosus* tapeworms (Andersen et al. 1978, 1979).

All samples were taken to the Parasitology Laboratory at Brigham Young University for examination of the collected material. The larger taeniids were transferred to new containers and then shipped to Kansas City, Missouri, where one of us (LAJ) identified the worms to species. The remaining fluid in each original sample bottle was divided into two equal portions and each part examined with a variable 7X-30X stereozoom microscope by a different investigator to detect the small *E. granulosus* tapeworms that might be present.

After the examinations and identifications were completed for each year of study, each dog owner was sent a letter detailing the results for each of his dogs and, when tapeworms were found, was also given an indication as to the most likely food item his dog had eaten to acquire such a tapeworm (e.g., sheep carcass, deer, rabbit, etc.). All data collected for each owner and each dog were entered onto tabular sheets designed for the project and then transferred to computer tapes. All categorization and tabulation of data were done on the Research VAX computer at BYU with the aid of Statistical Analysis Systems (SAS) programs. Analyses or statistical associations of specific cestode infections were tested for (1) effect of breed, sex, age of sheep dog, and number of sheep in individual herds; (2) occurrence in dogs owned by individuals who submitted animals for an examination either two or three years of the three-year study period; and (3) coexistence within all sheep dogs examined during the entire program.

Results

During the three-year study period, 269 separate sheep dogs were examined a total o

TABLE 4. Breed and sex of sheep dogs examined for cestodes, 1982–1984.

Breed	Sex		All dogs examined		Infected dogs	
	Male	Female	Number	Percent	Number	Percent
Australian Shepherd	4	6	10	2.9	5	3.7
Australian Shepherd cross	5	4	9	2.6	2	1.5
Border Collie	39	11	50	14.3	26	19.4
Border Collie cross	7	2	9	2.6	4	3.0
Blue Heeler	3	1	4	1.1	2	1.5
Blue Heeler cross	2	0	2	.6	1	.7
Collie	61	35	96	27.5	36	26.9
Collie cross	108	45	153	43.8	54	40.3
Dachshund cross	0	2	2	.6	0	0
German Shepherd	1	0	1	.3	0	0
German Shepherd cross	2	0	2	.6	1	.7
Kelpie	2	5	7	2.0	3	2.2
Poodle cross	3	0	3	.9	0	0
Terrier cross	0	1	1	.3	0	0
Total	237	112	349	100.0	134	100.0

TABLE 5. Age of sheep dogs examined for cestodes, 1982–1984.

Age of dog when examined	Number of separate examinations			Total examinations	Number of dogs infected	Percent of dogs infected
	1982	1983	1984			
0.5	10	27	26	63	14	22.2
1	19	21	17	57	22	38.6
2	16	31	19	66	32	48.5
3	12	18	16	46	20	43.5
4	9	10	10	29	10	34.5
5	4	10	8	22	10	45.4
6	3	6	6	15	8	53.0
7	5	4	2	11	5	45.4
8	4	3	3	10	4	40.0
9	3	2	2	7	2	28.6
10	4	3	5	12	3	25.0
11	1	2	2	5	3	60.0
12	0	3	0	3	0	0.0
13	0	0	1	1	1	100.0
15	1	1	0	2	0	0.0
Total	91	141	117	349	134	38.4

349 times; 205 dogs were examined only once, 48 dogs were examined two of the three years, and only 16 dogs were examined each of the three years (Table 1). Dogs were examined from 49 different owners, who had an average of 1,269 sheep each.

Tables 2 and 3 give various statistics as to the cestode infection levels identified within the dog population. Overall, 134 of 349 examinations (38.4%) showed at least one species of cestode present, whereas 215 examinations (61.6%) were negative. The level of infection in all examinations over the three-year period decreased from 49.5% in 1982 to 39.0% in 1983 to 29.1% in 1984 (Table 2). The infection levels for specific cestodes found over the three-year periods were: *Echinococcus granulosus*, 16 of 349 positive, 4.6%; *Taenia hydatigena*, 34 positive, 9.7%; *T. ovis krabbei*, 46 positive, 13.2%; *T. pisiformis*, 47 positive, 13.5%; and *T. serialis*, 24 positive, 6.9%. Specifically, the level of infection of *E. granulosus* dropped from 10 of 91 dogs positive (11.0%) in 1982 to 3 of 141 positive (2.1%) in 1983 and then rose slightly to 3 of 117 positive (2.6%) in 1984 (Table 3). The prevalence of

TABLE 6. Relative decline in cestode infections in sheep dogs examined, 1982–1984.

Cestode	Number of infections[1] 1982	1983	1984	Total	Gamma statistic	Standard error
Echinococcus granulosus	10	3	3	16	−0.522*	0.006
Taenia hydatigena	15	8	11	34	−0.208	0.156
Taenia ovis krabbei	13	21	12	46	−0.122	0.281
Taenia pisiformis	22	17	8	47	−0.440*	0.118
Taenia serialis	5	13	6	24	−0.047	0.176
Total:	65	62	40	67	Summary: −0.269	0.087

[1]Some dogs infected with more than one species of cestode.
*Statistically significant decrease (SAS program).

TABLE 7. Statistical associations (uncertainty coefficient; SPSSX) of specific cestode infections tested against breed, sex, age of sheep dog, and number of sheep in individual herds, 1982–1984.

Variable	Cestode	Uncertainty coefficient*	Standard error
Breed	*Echinococcus granulosus*	0.074	0.046
	Taenia hydatigena	0.055	0.031
	Taenia ovis krabbei	0.057	0.022
	Taenia pisiformis	0.042	0.016
	Taenia serialis	0.042	0.017
	Summary	0.029	0.013
Sex	*Echinococcus granulosus*	0.012	0.018
	Taenia hydatigena	0.006	0.010
	Taenia ovis krabbei	0.021	0.018
	Taenia pisiformis	0.001	0.006
	Taenia serialis	0.002	0.014
	Summary	0.003	0.004
Age	*Echinococcus granulosus*	0.164	0.046
	Taenia hydatigena	0.084	0.038
	Taenia ovis krabbei	0.077	0.032
	Taenia pisiformis	0.061	0.024
	Taenia serialis	0.061	0.028
	Summary	0.047	0.016
Number of Sheep	*Echinococcus granulosus*	0.141	0.049
	Taenia hydatigena	0.111	0.036
	Taenia ovis krabbei	0.143	0.028
	Taenia pisiformis	0.047	0.022
	Taenia serialis	0.092	0.019
	Summary	0.066	0.022

*Uncertainty coefficient values represent the reduction in uncertainty (1 to 0) in predicting the specific cestode infection when the specific test variable (i.e., breed, sex, age, or number of sheep) is known. All values are extremely low (i.e., indicate poor predictive capability).

infection for each specific cestode detected over the three-year study period is depicted in Figure 1.

The dog population surveyed could further be categorized into 14 different breeds (Table 4) and into 237 male and 112 female dogs. The most popular breeds examined were Border Collie (14.3%), Collie (27.5%), and Collie cross (43.8%). The age of the dogs was categorized into 15 age groups between 0.5 and 15 years of age (Table 5), with 66% of all examinations being done on dogs 3 years of age or less.

The age group categorization of dogs infected with *E. granulosus* showed that of 16 total infections over the three-year period, 3 each were identified in dogs one, two or three years of age; 2 infections in four-year-old dogs, four infections in six-year-old dogs, and one infection in an eight-year-old animal.

Statistical analyses of the trends in cestode infections over the three-year study period showed an over-all decrease (SAS; summary gamma statistic of −0.269), with individual decreases for all parasite categories. The greatest single decline in any species was for *E. granulosus* (gamma statistic of −0.522; Table 6). Additional statistical analysis showed that there were no significant correla-

TABLE 8. Statistical association (Wilcoxon Test) for cestode infections in sheep dogs of owners who submitted dogs for examination two of the three years of the study, 1982–1984.

Cestode	Number of owners[1]	Number of dogs examined		P value
		1st exam	2nd exam	
Echinococcus granulosus	7	10	1	0.036*
Taenia hydatigena	10	15	3	0.012*
Taenia ovis krabbei	11	14	7	0.036*
Taenia pisiformis	17	24	4	0.000*
Taenia serialis	5	6	2	0.109

[1] Owners identified in this table are those individuals who had dogs infected with specific tapeworms at an initial examination (either in 1982 or 1983) and then submitted dogs for examination also in a subsequent year (either in 1983 or 1984).
*Significant decrease at < 0.05 level.

TABLE 9. Statistical association (Quade Test) for cestode infections in sheep dogs of owners who submitted dogs for examination each year of study, 1982–1984.

Cestode	Number of owners[1]	Number of dogs examined			Statistical significance*		
		1982	1983	1984	1982 vs. 1983	1982 vs. 1984	1983 vs. 1984
Echinococcus granulosus	5	8	0	1	yes	yes	no
Taenia hydatigena	7	10	2	3	yes	yes	no
Taenia ovis krabbei	10	13	9	6	no	no	no
Taenia pisiformis	11	18	10	4	yes	yes	yes
Taenia serialis	3	4	8	1	no	no	no

[1] Owners identified in this table are those individuals who had dogs infected with specific tapeworms at an initial examination in 1982 and then submitted dogs for examination also in 1983 and in 1984.
*Significant decrease at < 0.05 level.

TABLE 10. Statistical association (Fisher's Exact Test) on coexistence of specific cestodes in all sheep dogs examined, 1982–1984.

Cestode	*Taenia hydatigena*	*Taenia ovis krabbei*	*Taenia pisiformis*	*Taenia serialis*
Echinococcus granulosus	.002*	.244	.461	.302
Taenia hydatigena	—	.790	.793	.492
Taenia ovis krabbei	—	—	1.000	1.000
Taenia pisiformis	—	—	—	.029*

*Significant positive association at < 0.05 level.

tions in any of the cestode infection categories over the three-year study period for breed, sex, or age of sheep dogs involved, nor with number of sheep owned by any individual rancher (Table 7). For owners who submitted dogs for two annual examinations during the three-year study period there was a significant decrease in the infection levels noted for *E. granulosus*, *T. hydatigena*, *T. o. krabbei*, and *T. pisiformis* (at 0.05 level; Table 8). For owners who submitted dogs for examination all three years of the study, a significant decrease in infection levels was noted for two of the three years for *E. granulosus* and *T. hydatigena* and for all three years for *T. pisiformis* (at 0.05 level; Table 9). A significant positive association in the coexistence of specific cestodes detected in the study was seen for *E. granulosus* and *T. hydatigena* and for *T. pisiformis* and *T. serialis* (at 0.05 level; Table 10).

DISCUSSION

Epidemiological factors on hydatid disease for this region, such as anthelmintic treatment regimes used in the dogs, sheep management practices, owner awareness of the life cycle and transmission of hydatid tapeworms, and willingness of local individuals to cooperate with recommended preventive and control measures for the region, had been previously evaluated (Schantz and Andersen 1980, Condie et al. 1981, Crellin et al. 1982, Andersen et al. 1983), and were not assessed in the present study. However, from the data collected in this project, several conclusions or trends can be identified.

Although it was relatively easy to convince ranchers to have their dogs examined for one year of our study, it became increasingly difficult to obtain their cooperation in subsequent years. A total of 19 of 49 separate owners submitted dogs for examination in only one of three years of the study, 10 owners had dogs examined two of three years, and only 20 owners submitted dogs all three years. Consequently, even though we examined 269 different dogs during the project, 205 were tested only one year, 48 for two years, and only 16 were examined each year of the three-year period. Part of the apparent reason for a decrease in repeat examinations was the inconvenience for ranchers to submit their dogs for examination when they needed the dogs on a daily basis. Generally dogs subjected to the rather harsh purgation used in our study were unable to do hard work for several hours following the examination, and sheep ranchers rapidly became aware of this complication. Furthermore, the field team of veterinarians could not always arrive at the camp site on a planned schedule, could not always find the herd in a specific locale, and sometimes could not traverse the mountainous roads which were on occasion interspersed with drifted snow even into mid-August.

Another factor which complicated our being able to examine more dogs in subsequent years was the rather high turnover of dogs in this particular industry. The age profile categorization showed a marked cluster of dogs in the early age brackets, with 66% being three years of age or less. Reportedly, many dogs are lost or stray from the camp sites, some are purposefully destroyed when they do not prove to be easy to train, some are accidentally killed (e.g., being run over by owner's truck), and some cannot withstand the rigors of that type work for more than a few months at a time. Dogs in the latter category are routinely taken to the home residence of the owner and are allowed to recuperate for several weeks before being returned to the mountain rangeland. This decrease in dogs examined on a year-to-year basis naturally complicated our attempts to accurately identify the prevalence of cestodes in this population of animals and to properly evaluate our overall program. However, for those owners who did submit dogs for more than one year, there was a significant reduction in specific cestodes identified (Tables 8 and 9), which fact suggests that such owners were implementing recommended preventive and control measures in their overall sheep and dog management.

The study also showed that the same group of cestode species was identified in these sheep dogs for all three years, as shown in previous surveys (Andersen et al. 1973, Loveless et al. 1978, Jensen et al. 1982). Of particular importance was the fact that the greatest individual reduction in prevalence of any one species of cestode was observed for *E. granulosus* (gamma statistic of −0.522) and suggests that ranchers are indeed concerned about hydatid disease. The observed reduction in the prevalence of *T. hydatigena* (gamma = −0.208) should have paralleled more closely that of *E. granulosus*, since sheep serve as the principal intermediate host in the life cycle of both parasites. Jensen et al. (1982) found that 25 of 76 mule deer (32.9%) examined in central Utah harbored cysticerci of *T. hydatigena,* which fact could account for the availability of an additional source of infection (other than sheep) for dogs in that region. A consistent drop in the infection level also occurred for *T. pisiformis* (gamma = −0.440), where the numbers of infected dogs dropped from 22 in 1982 to 17 in 1983 to 8 in 1984. Such a decline could have been due to a drop in the rabbit (intermediate host) population, since rabbits go through regular fluctuations in numbers.

We did not see any statistical correlation in this study of specific cestode infections with breed, sex, and age of sheep dogs (Table 7) However, we did note a significant positive association on coexistence of *E. granulosus* and *T. hydatigena* and also of *T. pisiformis* and *T. serialis* (Table 10). The fact that the firs two species of cestodes utilize sheep as principal intermediate hosts and that the second two use rabbits in that role corroborates the presumed dietary habits of the dogs harboring these cestodes and adds additional validation to the specific identification of the cestode reported over the three-year period.

With the mountainous terrain in this region and the large numbers of sheep present, it i unlikely that ranchers will ever be able to identify all sheep that die or are killed on the grazing sites, nor will they be able to burn or bury all carcasses. However, our observations over the past several years have indicated that more ranchers are now using an increased amount of commercial food for their dogs rather than expecting them to scavenge for food, and that fewer sheep are now butchered for routine consumption by the herders than in former years. These practices would definitely reduce the availability of sheep viscera to sheep dogs at the camp site.

The probable advantage of using praziquantel in our program to treat all dogs in the region, irrespective of whether or not they proved to be infected with cestodes, is somewhat difficult to evaluate with the design of our project, and in particular with the lack of large numbers of repeat examinations. Inasmuch as the time required for adult worms to develop and become patent after cystic material is eaten by the dog is only 40–45 days (Rausch 1975), and since our program monitored the dogs only once per year, we are unable to substantiate the known efficacy of praziquantel as demonstrated in experimentally infected dogs (Andersen et al. 1978, 1979, Andrews et al. 1983). Nevertheless, our data show that there was a definite decline in the overall cestode infection level during the three-year study period, and a more frequent program of drug administration may be warranted. The use of praziquantel in our study was a clear signal to the owners and herders that chemotherapy must be incorporated into an overall program to prevent and control hydatid disease. Certainly the use of this particular drug would have had some contributory effect to the general downward trend in levels of cestode infection noted. Recent testing in our laboratory on the efficacy of a new paste formulation of praziquantel (Andersen et al. 1985) will be an additional benefit to the ranchers in this particular region, because they will soon be able to purchase and use that formulation rather than to rely on either tablet or injectable formulations. Tablets are frequently difficult to administer to certain unmanageable dogs, and injectable formulations require an assortment of needles and syringes or the services of an attendant veterinarian.

In spite of the difficulty in completing this particular surveillance project, the general attitude and cooperation of the owners and herders remained positive throughout. This same attribute has been evident from the very beginning of the hydatid disease control program in Sanpete County in 1971 and is undoubtedly the most important factor in whatever level of success the program has achieved. Inasmuch as the control program we have attempted to implement has been an entirely voluntary campaign, it has been essential that all measures advocated or undertaken be promoted in a cooperative and friendly manner. Many local individuals such as community and church leaders, educational administrators and teachers, public health workers, and local veterinarians and physicians have all contributed markedly to the success of the program. The incorporation of a filmstrip and coloring books on hydatid disease into the school curricula has definitely enhanced the educational aspect of the campaign (Crellin et al. 1982, Andersen et al. 1983). However, since the last surgical case for removal of hydatid cysts from an individual in Sanpete County occurred in 1979 (Crellin et al. 1982), it is important the complacency during an era of diminished public health emphasis not be allowed to occur. In 1971, 20%–25% of the dogs in several communities were infected with *E. granulosus* (Andersen et al. 1973), whereas it is now virtually impossible to find infected dogs from these same communities. Also, in 1971 approximately 10% of all sheep slaughtered at local abattoirs in central Utah had hydatid cysts (Andersen and Wallentine 1976), whereas 14 years later the number of sheep reported to have hydatid cysts is well below 1% of those slaughtered, and only rarely is it possible to collect hydatid cysts from abattoirs in this region. In 1984 only three dogs infected with *E. granulosus* were identified along the Skyline Drive, yet one of the dogs had the heaviest natural infection seen to date in this county. This dog could well have been a source of infection for at least several sheep grazing in that herd, which in five to seven years could be the potential source for continued transmission to other dogs. If such a focus of infection is perpetuated, the chance for eventual human cases originating from any one dog source would be greatly increased. Thus, the project now terminates with a possible "tip of the iceberg" still evident.

It now seems that most of the individuals living in Sanpete County have had ample opportunity to become educated about hydatid disease and the distinct characteristics that allowed the disease to become endemic in that region. Whether or not a concerted effort will continue by both individuals and community leaders in attempting to implement recommended preventive and control measures for hydatid disease in central Utah remains to be seen. Hydatid disease has been controlled or eradicated completely in parts of the world such as Iceland and on the Island of Cyprus, but extensive efforts to eradicate the disease elsewhere, such as in an endemic site in New Zealand, have not succeeded entirely (Gemmell 1979). Many of the unique characteristics and epidemiological determinants which were identified for Sanpete County (Crellin et al. 1982) still exist. The only major factor that has changed through time has been the increase in public awareness and basic knowledge on the life cycle of the causative parasite. It is hoped management practices for both dog and sheep populations in Sanpete County will be modified sufficiently as to indeed decrease the potential for human cases in the future.

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DAM-RAISED FAWNS, AN ALTERNATIVE TO BOTTLE FEEDING

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Abstract.—Rearing young ungulates for ecological studies is costly and time consuming. Doe-rearing mule deer (*Odocoileus hemionus*) fawns is a viable alternative to the common method of bottle-feeding. Fawns tamed while nurtured by their tractable dams showed no marked difference in tractability over bottle-reared orphans. The advantages of doe-rearing are better health for the young and convenience for the handler.

The use of tame animals to obtain information on the foraging behavior and habitat selection of wild ungulates is increasing. This technique has been used with many native North American species (Reichert 1972) as well as several from Africa (Hutchison 1970). Close observation of foraging animals offers more precise dietary assessment than fecal/rumen sample analyses or distant observation, yet time and monetary investments required to rear and train experimental animals are high. Several methods for successfully rearing tractable animals have been reported. The most common is bottle-raising captured neonates (Schwartz et al. 1976, Hobbs and Baker 1979, Addison et al. 1983) or the young born to either penned wild or tame dams (Reichert 1972, Knorre 1974). Another option is taming wild-caught yearlings, as discussed by Kreulen (1977).

The Utah Division of Wildlife Resources has maintained a tame mule deer (*Odocoileus hemionus*) herd for more than 30 years by bottle-feeding fawns. In the last three years 14 fawns have been tamed while nurtured by their dams. We report this as a viable alternative to bottle-rearing of young, with advantages in better health and convenience.

Rearing

The herd was maintained in a 1-ha compound on the foothills of the Bear River Range at Logan, Utah. Beginning in early June the does were carefully observed for signs of impending parturition. They were then put into separate 5 x 25 m outdoor runs each with an open-air shed and hay bedding. The fencing must be stout to withstand aggressive behaviors between does and of a fine mesh wire on the bottom meter to prevent fawns from escaping. The sheds were cleaned of soiled bedding daily to reduce development and spread of disease. Green alfalfa hay, barley, balanced-ration pellets, and clean water were available ad libitum. To supplement the sparse forage growing in the runs, the animals were given freshly clipped mixed forbs (mostly alfalfa) morning and evening for a month postpartum and whenever a source was available thereafter. As noted by Schwartz et al. (1976) for pronghorn (*Antilocapra americana*) fawns, the deer fawns also consumed small quantities of soil beginning at about one week of age.

When possible, births were attended to assure the health of both fawn(s) and doe and to ensure that the fawn(s) obtained colostrum. If the doe did not attend the young, they were removed and subsequently bottle-raised. However, the inability to provide milk alone did not dictate bottle-rearing. The doe's licking of the perianal region stimulated the fawn to seek out a teat (or nipple) and nurse. This response could be used to advantage when supplemental bottle-feeding was required. One doe, with mastitis, cleaned her fawn while it nursed from a bottle. This doe-handler cooperation carried through until weaning.

During the first week does were kept with their fawns 24 hours a day. The young were exposed to a minimum of 3 hours human contact and gentle handling per day. By the second week does were turned out in the morning, returned at noon to clean and nurse their young, turned out again in the afternoon, and put in for the night in the evening. Generally, from the third week until fawns were weaned at three months, the dams were eager to get out in the mornings and were left out until evening. Any fawn handling or training could proceed as described by others (Reichert 1972, Parker et al. 1984).

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HEALTH

The most common diseases encountered were of intestinal microbes causing diarrhea leading to rapid dehydration, emaciation, and death. Although Kramer et al. (1971) discussed the occurrence of *Escherichia coli* in mule deer, and Schwartz et al. (1976) found *Clostridium perfringens* to be a problem in pronghorn, our major concern was with *Coccidia* spp. Upon detection of this protozoan, 12.5% sodium sulfamethazine was used to prevent and treat the *Coccidia* infections. The drinking water was treated for two days with 8ml/l water (1 oz/gal) at time of birth, at one week postpartum (when the fawns begin drinking water), at two weeks, and anytime thereafter when loose or watery feces were noticed. A change in the character of the feces is the cue to an intestinal infection. For a more detailed discussion of the normal changes that the feces of young growing fawns undergo see Schwartz et al. (1976).

Although sulfamethazine is commonly used on livestock, Schwartz et al. (1976) noted that the drug may crystalize in the urine and kidneys of young animals. As an alternative they recommended the use of Sulfaquinoxaline. Sulfamethazine was effective in controlling diarrhea in all the nine fawns treated and we have, as yet, experienced no adverse effects. We do, however, recommend caution in the use of this drug.

In their evaluation of fawn-rearing procedures, Halford and Alldredge (1978) concluded that doe-reared fawns had no health advantage over those bottle-raised. They experienced 67% (6 of 9 total) mortality of dam-raised fawns to necrobacillosis (*Fusibacterium necrophorum*), whereas the mortality of hand-raised fawns was only 33% (3 of 9 total), entirely due to *E. coli* and *Streptococcus* spp. umbilical infections. Unlike the hand-raised fawns, however, 6 of the 9 dam-raised fawns (67%) were: (1) kept in pens with no forbs or grasses available, (2) at higher animal densities, and (3) nursing does that had been on deficient diets. As reviewed by Hibler (1981), necrobacillosis is often associated with poor range and crowded conditions. Therefore, the losses due to this disease, as well as many others, may well be averted under better conditions.

DISCUSSION

Over three years 14 fawns have been raised by does, and we bottle-reared 7 orphans. There was no notable difference in the tractability of the animals reared by these two methods, but there was a marked difference in favor of dam-reared fawns in their stature as yearlings and two-year-olds. This was particularly noticeable in those raised as singles rather than twins by their dam. If given a choice, raising singles is preferable. They exhibited a faster growth rate and were generally more robust than twins. In addition, the lactation drain on the doe was greatly reduced.

Our visual assessment agreed with Halford and Alldredge (1978), who reported significantly higher ($P < .001$) mean body weight and growth rates of fawns raised by their dam as compared to those bottle-reared. Our yearling bucks were equal to or larger in statur than the bottle-raised two-year-olds and wer of substantially heavier build than their bottle-raised cohorts. A more quantitative indication of physical condition is the minimum breeding age of females (Mackie et al. 1982) Of two doe fawns sired by the same buck an raised concurrently, the dam-raised one gav birth to a fawn at one year of age. This is a rar occurrence and was not matched by her bottle-fed half sister.

There are two major advantages of doe rearing fawns: (1) health—there is no subst tute for the dam's nurturing, species specifi colostrum, and doe's milk, which has twic the nutritional value of cow's milk (Sho 1981), and (2) time—time and inconvenienc spent in cleaning and preparing bottles thre to five times daily is eliminated, thus allowin more time for direct contact with the young.

It is unknown whether a key period for imprinting on a handler exists. Our fawns were first exposed to humans between 0 and 24 hours after birth. The animals were predominately handled by two people, yet were in frequent contact with others. Several authors stress the bond formation between handlers and bottle-raised young (Schwartz et al. 1976, Addison et al. 1983). Without the dependence on a handler for feed, the development of confidence between handlers and dam-reared fawns is very important. Initially, preferential behavior was exhibited toward the handlers; yet, amity or distrust did develop toward anyone with whom the animals had contact. The fawns' response to individuals gradually moderated through their first year.

The work reported herein was done with fawns born to tractable does. The presence of tame conspecifics eases the handling of new animals (Kreulen 1977). Some species, though, may not be suited for this method of rearing. As part of a project involving white-tailed (*Odocoileus virginianus*), mule, and black-tailed (*O. h. columbianus*) deer in New Hampshire, an effort was made to raise two sets of twin white-tailed deer fawns on their dams. The does were the most tame of the herd; however, their fawns were never approachable despite constant human contact. One set eventually brought about their own deaths in panicked flight (P. Pekins, personal communication). In time the adaptable species will be known. Until then dam-raising young should be considered as an option when rearing animals for ecological studies.

ACKNOWLEDGMENTS

We thank M. Urness for assistance in rearing of fawns; K. Udy and M. Powell for veterinary advice; and J. C. Malechek, F. D. Provenza, and M. L. Wolfe for helpful suggestions and review of this manuscript. Facilities, animals, and funding were provided by the Utah Division of Wildlife Resources through Federal Aid Project W-105-R.

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SUBSPECIFIC IDENTITY OF THE AMARGOSA PUPFISH, *CYPRINODON NEVADENSIS*, FROM CRYSTAL SPRING, ASH MEADOWS, NEVADA

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Abstract.—Samples of pupfish from Crystal, Marsh, and Point of Rocks springs, Ash Meadows, Nevada, were examined to determine the subspecific identity of *Cyprinodon nevadensis* presently inhabiting Crystal Spring. Meristic and morphometric analyses indicate that Crystal Spring is inhabited by *C. n. mionectes*. The presence of this subspecies is most likely explained by their precarious survival in the spring's outflow after they were eliminated by transplanted largemouth bass in the spring pool, and their subsequent reestablishment throughout the spring system after the extirpation of the bass.

Crystal Spring (= Big Spring of Miller 1948) is the type locality for the Ash Meadows pupfish, *Cyprinodon nevadensis mionectes* Miller. Crystal Spring was chosen by Miller (1948) as the type locality because its pupfish population "has characters which very closely approach the average for the subspecies as determined by an analysis of all populations." In recent years, however, the subspecific identity of the pupfish in Crystal Spring has been questioned.

On 1 January 1966, J. E. Deacon, C. L. Hubbs, and R. R. Miller searched Crystal Spring for pupfish and found none (J. E. Deacon, field notes; Miller 1969). However, at least 10 transplanted largemouth bass, *Micropterus salmoides*, were seen in the main spring pool. The pupfish population "reappeared" by early February 1975 (Liu and Soltz 1983) and was later described as in "fine shape" with a population of approximately 1,500 pupfish (Hardy 1980).

Two subspecies of *Cyprinodon nevadensis* occur in Ash Meadows. In addition to its presence in Crystal Spring, *C. n. mionectes* occurs in a variety of lower-elevation springs (Miller 1948, Soltz and Naiman 1978). Among other springs, *Cyprinodon n. mionectes* occurs in Jack Rabbit, Point of Rocks, the Bradford Springs, and springs at the northern end of Ash Meadows that discharge water into the formerly vast Carson Slough area. Several of these springs, and an introduced population of *C. n. mionectes* at Collins Ranch (Baugh et al., in press), are within 3 km of Crystal Spring. *Cyprinodon n. pectoralis* also occurs in nearby springs, such as Indian, Marsh, School, and Scruggs. The population of *C. n. pectoralis* from Indian Springs was particularly suspect as a source for the Crystal Spring population because that spring's outflow frequently discharges into the outflow of Crystal Spring. Both subspecies of *Cyprinodon nevadensis* are listed as endangered by the U.S. Fish and Wildlife Service.

The potential for surface water connection among the various springs is compounded by periodic flash floods, which may distribute pupfish some distance from their usual habitat, and by the formation of Crystal Spring Reservoir, which is fed by outflow water from Crystal Spring.

Thus, at least three hypotheses can be employed to explain the recurrence of pupfish in Crystal Spring:

1. pupfish from another spring reached Crystal Spring by surface water connection,
2. pupfish from another spring were introduced into Crystal Spring by man, or
3. the pupfish in Crystal Spring were not eliminated by the largemouth bass but only reduced to such low numbers that they appeared to be extirpated.

Because of the geographic proximity of other springs, either of the first two hypotheses could explain the presence of either *C. n*

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mionectes or *C. n. pectoralis* in Crystal Spring. The latter hypothesis, of course, would only be appropriate for explaining the presence of *C. n. mionectes*. The purposes of this report are to determine the subspecific identity of *C. nevadensis* presently inhabiting Crystal Spring and to explain their occurrence.

MATERIALS AND METHODS

Meristic and morphological characters were utilized to compare the unknown *C. nevadensis* from Crystal Spring to populations of *C. n. mionectes* from Point of Rocks Springs and *C. n. pectoralis* from Marsh Spring. The two previous taxonomic studies of *C. nevadensis* from Ash Meadows have documented that the number of pectoral fin rays and number of preopercular pores in the cephalic lateral-line system are diagnostic in separating the two subspecies (Miller 1948, Miller and Deacon 1973). These two characters plus the structure of the preopercular canal were used to determine the identity of the Crystal Spring population.

Thirty specimens longer than 25 mm SL were analyzed from each of the following three collections of *C. nevadensis* made 17 January 1985 by T. M. Baugh and J. W. Pedretti:

1. UMMZ 213444. 59 *Cyprinodon nevadensis* ssp. (26.6–37.9 mm SL) from Crystal Spring.
2. UMMZ 213445. 60 *Cyprinodon nevadensis mionectes* (22.8–35.6 mm SL) from Point of Rocks Springs.
3. UMMZ 213446. 60 *Cyprinodon nevadensis pectoralis* (21.2–39.3 mm SL) from Marsh Spring.

Samples from Point of Rocks and Marsh Spring were chosen because of their geographic proximity to Crystal Spring. Also, Marsh Spring is adjacent to Indian Springs and should closely represent any *C. n. pectoralis* that may have entered Crystal. No meristic data are available for *C. n. pectoralis* from Indian Springs. The "Indian Spring" referred to in Miller and Deacon (1973: Fig. 1 and text) clearly is Marsh Spring. The two spring systems are in close proximity. Marsh Spring is located more northerly and its outflow is partially impounded by a small reservoir.

The methods of Miller (1948) were employed with the exception that only the left pectoral fin rays were counted. Counts of the left and right preopercular pores were separated from some analyses so that a count of 7-6, for example, refers to a specimen with 7 preopercular pores on the left side of the head and 6 preopercular pores on the right. Otherwise, counts on the left and right sides were combined.

RESULTS AND DISCUSSION

After all counts were completed, results from known samples of *Cyprinodon n. mionectes* and *C. n. pectoralis* were compared to previous results of Miller (1948) and Miller and Deacon (1973). Results from all studies were expected to be very similar because the methodology for performing the counts was nearly identical.

Counts of the diagnostic meristic characters of the Point of Rocks Springs population of *C. n. mionectes* were very similar to those given by Miller (1948) (Tables 1 and 2). Pectoral fin rays were modal at 16 in both studies and averaged 15.68 for Miller (1948) and 15.73 (present study). Counts of preopercular pores were modal at 12 for both studies but averaged slightly higher in Miller (1948) than in this study (12.54 v. 12.17, respectively).

Counts of the diagnostic meristic characters of the Marsh Spring population of *C. n. pectoralis* also were very similar to the earlier studies (Tables 1 and 2). The number of pectoral fin rays were modal at 17 and averaged 16.61 (Miller and Deacon 1973) and 16.50 (present study). Although the presence of 17 v. 16 pectoral fin rays is the primary character that separates *pectoralis* from *mionectes*, the Marsh Spring population of *C. n. pectoralis* has a higher frequency of individuals with 16 pectoral fin rays than other populations within the subspecies (Miller and Deacon 1973). Previous data on preopercular pore counts for the Marsh Spring population were lacking, so data from this study were compared to preopercular pore counts of the typical form of the subspecies from School Spring. Preopercular pore counts averaged 13.36 in the School Spring sample (= Lovell's Spring of Miller 1948) and 13.30 in the Marsh Spring sample (present study).

TABLE 1. Comparison of pectoral fin-ray counts of *Cyprinodon nevadensis* from three springs in Ash Meadows, Nye County, Nevada.

		13	14	15	16	17	18	x̄
Crystal Spring	Miller 1948: Table 16, 1942		8	102	112	11		15.54
	present study, 1985		1	10	18	1		15.63
Point of Rocks Springs	Miller 1948: Table 16, 1942	1	3	65	112	12		15.68
	present study, 1985		2	8	16	4		15.73
Marsh Spring	Miller and Deacon 1973:137				24	30	2	16.61
	present study, 1985			1	13	16		16.50

TABLE 2. Comparison of preopercular pore counts of *Cyprinodon nevadensis* from four springs in Ash Meadows, Nye County, Nevada.

		10	11	12	13	14	15	16	x̄
Crystal Spring	Miller 1948: Table 26, 1942		1	39	18	8			12.50
	present study, 1985		3	18	8	1			12.23
Point of Rocks Springs	Miller 1948: Table 26, 1942	1	2	55	20	18			12.54
	present study, 1985		3	21	5	0	1		12.17
School Spring	Miller 1948: Table 26, 1939		1	24	18	54	1	2	13.36
Marsh Spring	present study, 1985		1	7	10	8	2	2	13.30

A comparison of pectoral fin-ray numbers in the three 1985 collections indicates that the Crystal Spring population is *C. n. mionectes* (Table 1). A similar conclusion is reached when comparing the number and frequency of preopercular pore counts (Table 2). The Crystal Spring sample of *C. nevadensis* averaged 15.63 pectoral fin rays and 12.23 preopercular pores. Both values are within the results expected for *C. n. mionectes*.

The Crystal Spring sample of *C. nevadensis* was modal at 16 pectoral fin rays but included a relatively large percentage (33%) of individuals with 15 pectoral fin rays. This contrasts sharply with the Marsh Spring sample of *C. n. pectoralis*, which was modal at 17 pectoral fin rays and contained a relatively large percentage (43%) of individuals with 16 rays and only one fish with 15.

The Crystal Spring sample of *C. nevadensis* averaged 12.23 preopercular pores. This value is very similar to the average number of preopercular pores in the Point of Rocks Springs sample (12.17) but is quite distinct from the average in the Marsh Spring sample (13.30). The modal number of preopercular pores in the Crystal Spring sample is 12. This agrees with the value from the Point of Rocks sample but again contrasts with results from Marsh Spring, where those pores are modal at 13 (Table 2). Preopercular pore counts, with frequency of counts given parenthetically, are as follows for Point of Rocks: 5-6 (1), 6-5 (2), 6-6 (21), 6-7 (3), 7-6 (2), 8-7 (1); Crystal: 5-6 (2), 6-5 (1), 6-6 (18), 6-7 (2), 7-6 (6), 8-6 (1); and Marsh: 5-6 (1), 5-7 (1), 6-6 (6), 6-7 (5), 7-6 (5), 7-7 (8), 8-7 (2), and 8-8 (2).

The structure of the preopercular canal also varied significantly between the Point of Rocks Springs and Crystal Spring samples, and the *C. n. pectoralis* from Marsh Spring. In the Marsh Spring sample, 13% of the fish possessed at least one interrupted preopercular canal. Both the left and right canals were interrupted in one specimen. Although interruption of the canal results in a higher pore count, the primary causal factor in the higher pore counts in the March Spring population was the presence of a seventh pore on the anterior end of the preopercle. Most *C. n. mionectes* contain only 6 pores on each side. No preopercular canal interruption was noted in *C. n. mionectes* from Point of Rocks or Crystal springs, although one specimen from Crystal Spring possessed an open canal on one side.

Delays in completion of the cephalic canal system until adulthood have been noted for certain cyprinodonts (Hubbs and Miller 1965) and could possibly explain some of the above differences noted between *C. n. mionectes* and *C. n. pectoralis*. Differences in standard length among the subsamples examined, however, are slight. Ranges and means of standard length for the subsamples examined are: Point of Rocks Springs, 26.8–35.6 mm (x̄

= 30.98); Crystal Spring, 28.3–37.9 (33.26); and Marsh Spring, 25.3–39.3 (29.48).

Finally, the meristic characters of the Crystal Spring sample were compared to data from the original study of the Crystal Spring population by Miller (1948). Very close agreement is seen in the average number of pectoral fin rays observed in the Crystal Spring sample taken in 1942 (Miller 1948) and in 1985 (present study) (Table 1). The 1942 sample averaged 15.54 rays, whereas the 1985 sample averaged 15.63. A similar agreement is seen in the number of preopercular pores from samples collected in 1942 and 1985 (Table 2). The 1942 sample included 59% of individuals with 12 preopercular pores and 27% with 13. The 1985 sample contained 60% of individuals with 12 preopercular pores and 27% with 13.

Based on the results of this study, the subspecific identity of the pupfish from Crystal Spring is *C. n. mionectes*. It appears that the present *C. n. mionectes* population is descended from those individuals who withstood the pressure from largemouth bass. The question as to whether the present Crystal Spring population persists by natural occurrence, was introduced, or made its way by surface water connection from another *C. n. mionectes* population may be answered as follows. Although the predaceous largemouth bass apparently eliminated *C. n. mionectes* from the spring pool at Crystal, it may be that some pupfish survived in the spring outflow. According to field notes of one of the authors (JED 66-1), only 100 yards of the outlet ditch were searched. Robert R. Miller (10 October 1985 in litt. to JEW) supported the hypothesis that *C. n. mionectes* may not have been eliminated from the entire spring system and stated, in part:

> to say unequivocally that *Cyprinodon* was gone from this system [Crystal] would be awfully hard to defend. In frigid midwater [ice on ground, 1 January 1966] you might not expect to see pupfish, especially when they had been impacted for X-years by that dastardly predator *Micropterus salmoides*. Granted that the pupfish could certainly have been wiped out at the main spring pool. I think it is unjustified to assume they were eliminated throughout the long outlet ditch as well.

The causes of disappearance of largemouth bass from Crystal Spring are uncertain as well. The warm water (30.9 C) of the spring pool may have inhibited reproduction, though such would not be the case throughout the cooler outlet ditch and reservoir. This, coupled with constant angling pressure by the workers in Ash Meadows, may have eliminated bass from the spring system. Regardless of the causes, it is quite reassuring to know that the type locality of *Cyprinodon nevadensis mionectes* still harbors that unique form of pupfish and that the spring has rid itself of the introduced bass.

ACKNOWLEDGMENTS

We appreciate the efforts of Tom M. Baugh and John W. Pedretti in collecting the pupfish used in this study. Reviews of this paper by Robert R. Miller, Cynthia D. Williams, and Donna L. Withers are gratefully acknowledged. Also, permission to quote from Miller's insightful missive is appreciated.

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TWO ABERRANT KARYOTYPES IN THE SAGEBRUSH LIZARD (*SCELOPORUS GRACIOSUS*): TRIPLOIDY AND A "SUPERNUMERARY" ODDITY

Pamela Thompson[1,2] and Jack W. Sites, Jr.[1]

Abstract.—Widespread karyotypic sampling in the lizard *Sceloporus graciosus* Baird & Girard has confirmed previous reports of chromosomal monotypy. Most individuals throughout the range have a diploid karyotype of 2N=30 consisting of 12 biarmed macrochromosomes and 18 microchromosomes. A single female karyotyped from the vicinity of Riverside, California, was unmistakably triploid, showing 3N=45 with 18 macrochromosomes and 27 microchromosomes. This female appeared phenotypically normal but appeared reproductively incompetent. A male from Zion National Park, Utah, showed an extra bivalent in some diakinesis arrays, which apparently represents a supernumerary chromosome.

A major study is currently in progress to determine the population genetic structure of the chromosomally monotypic sagebrush lizard, *Sceloporus graciosus* Baird & Girard. In this study 112 individuals from seven western states (AZ, CA, CO, ID, NV, UT, WY) were karyotyped to confirm chromosomal monotypy, and all but two individuals showed the previously reported 2N=30 normal karyotype (Cole 1971, 1975a, Jackson and Hunsaker 1970). One showed a triploid karyotype, and another possessed an extra bivalent in diakinesis spreads. The former represents the third known case of unusual triploidy in a species of *Sceloporus*, and the latter may be an example of a supernumerary chromosome.

Methods

Lizards were captured alive by noosing or by stunning with rubber bands. Karyotypes were prepared according to Baker et al. (1982) from testes, in the case of reproductively active males, or from bone marrow in the case of juveniles, females, or postreproductive males. Prior to karyotyping the lizards were injected with a yeast-sugar solution (Cole and Leavens, 1971) to increase the mitotic index. Treated suspensions of bone marrow or testes cells were dropped onto clean microscope slides and stained with a 6% Giemsa phosphate solution (Patton 1967). At least five metaphase spreads were scored on most individuals.

Results

Of the 112 lizards we karyotyped, 110 showed the normal 2N=30 karyotype, which consisted of 12 metacentric or submetacentric macrochromosomes (12M) and 18 microchromosomes (18m) (Fig. 1A). Macrochromosome pair two in metaphase cells with elongate chromosomes frequently showed terminal satellites (see arrow Fig. 1A) similar to those reported by Cole (1971) for this species. One adult female showed a triploid karyotype, 3N=45, consisting of 18 meta- or submetacentric macrochromosomes, and 27 microchromosomes. (Fig. 1B).

Diakinesis arrays from testes of 90 reproductively active males almost always consisted of six macrochromosomal and nine microchromosomal bivalents (Fig. 1C). One adult male, however, showed one extra microchromosomal bivalent in seven of 44 cells examined (Fig. 1D). Seven other arrays showed the more typical nine microchromosomal bivalents, while the remaining 30 spreads were incomplete.

Discussion

Karyological work done on S. *graciosus* includes 17 specimens examined by Cole (1971, 1975a) from Arizona, California, Colorado, New Mexico, and Utah, five specimens examined by Jackson and Hunsaker (1970) from California, and 112 specimens examined by us

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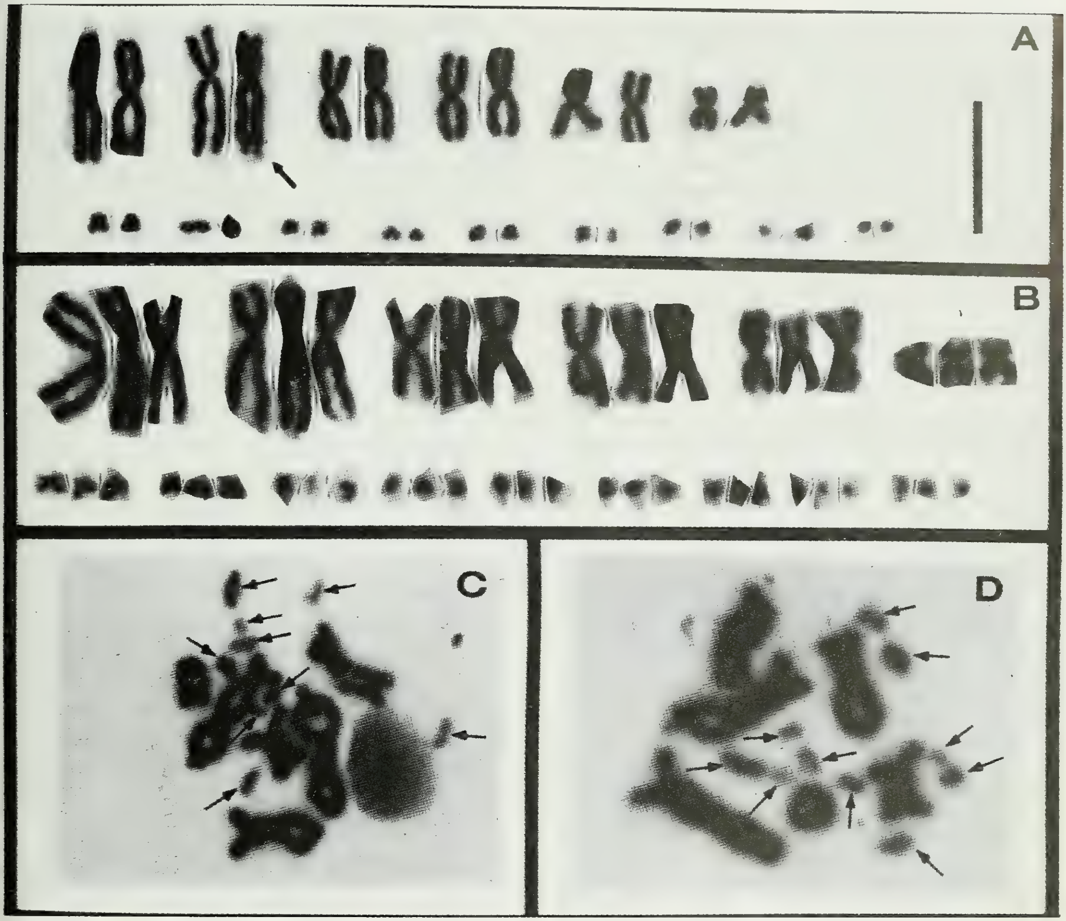

Fig. 1. Karyotypes of *Sceloporus graciosus*. Bar represents 10 μm for all karyotypes. A, Normal 2N=30 (12M + 18 m) karyotype with terminal satellites (see arrow) on pair two (juvenile, BYU 37620). B, Triploid 3N=45 (adult female, BYU 38201). C, Normal diakinesis array showing nine microchromosomal bivalents, (adult male, BYU 37975). D, Diakinesis array showing extra "bivalent" (adult male, BYU 37608).

from the above states as well as Idaho, Nevada, and Wyoming. Of 134 individuals karyotyped thus far, only two individuals with the anomalies illustrated above (Fig. 1B, 1D) deviate from the normal 2N=30, 12M + 18m pattern. Since both the anomalous individuals were single isolated cases within their respective population samples (the triploid was one of seven individuals karyotyped from San Bernardino County, California, and the individual with an extra chromosomal bivalent was one of seven specimens karyotyped from Zion National Park, Utah), it is likely that these cytotypes are not widespread.

Most reported cases of triploidy in lizards are associated with parthenogenetic populations or species that are thought to have originated by interspecific hybridization (Bickham 1984, Cole 1975b, 1984, Hall 1970). However, isolated cases of triploidy have been found in nonparthenogenetic lizard species. A single aberrant triploid individual was reported by Witten (1978) in the Australian agamid *Amphibolurus nobbi*. Additional cases of triploidy have been reported for two species of *Sceloporus*. From a sample of 1,300 lizards karyotyped, Hall (1973) scored four triploid individuals of the chromosomally variable *S. grammicus* complex. Three of these were males of three different chromosome "races" or cytotypes. The fourth, a female discovered in a hybrid zone between two cytotypes, possessed two chromosome sets from one parental cytotype and one from the other. The hybrid nature of this karyotype led Hall to suggest that this female may represent an incipient parthenogen. The second example in the genus *Sceloporus* was a triploid adult female of *S. occidentalis* reported by Cole (1983) from a sample of 16 individuals karyotyped from the Pine Valley Mountains of southwestern Utah. At this locality *S. occidentalis* occurs sympatrically with three other species of *Sceloporus*, but there was no evidence that interspecific hybridization was involved in the production of this triploid. Furthermore, comparative study of the reproductive tracts of other adult *S. graciosus* collected the same day indicated that the triploid was sterile, having small unplaited oviducts compared to the broadly plaited oviducts and yolked follicles of the other females.

The triploid example we report herein appears also to be an aberrant individual of nonhybrid origin, as all three haploid sets are morphologically typical of *S. graciosus* (Fig. 1B). This individual appeared to be a phenotypically normal adult female. The range of the four scale counts plus body length taken from all females collected from the San Bernardino County locality (N=5) are as follows (triploid value in parentheses): (1) scales around midbody, 50-61 (50); (2) dorsal scale count, 48-53 (50); (3) total fourth toe lamellae, 46-50, (50); (4) total supraoculars, 13-15 (14), and (5) (snout vent length, 56-60 mm (56). A noticeable difference was observed, however, in the reproductive condition of these five females. Whereas the four diploids possessed visible paired oviducts and either a shelled egg (in the case of one female) or small clusters of yolked eggs, the triploid uniquely possessed massive fat reserves and lacked visible paired ovaries and oviducts. We interpret this as sterility in the triploid female.

We suggest that these three isolated instances of aberrant triploid individuals (in *Sceloporus*) be interpreted simply as reproductive accidents (the fusion of a reduced with an unreduced gamete), not as incipient parthenogenesis, unless there is clear evidence of reproductive viability and the thelytokous production of all-female offspring.

The male who possessed an extra bivalent in some of its diakinesis arrays is more difficult to interpret, as there are no metaphase spreads or secondary spermatocytes available for this individual. The simplest explanation is that this extra element represents a single supernumerary or B-chromosome. It might also represent an extra microchromosomal bivalent, although the resolution on our slides does not permit this distinction to be made. The fact that not all cells possessed this extra element suggests that, if it is a B-chromosome or extra bivalent, it is not being distributed to all cells after mitotic division. We stress the very tentative nature of our interpretation and recognize the need for additional meiotic and C-band studies (see Patton, 1977, for a recent example with rodents).

ACKNOWLEDGMENTS

We thank Dr. Robert Bezy, Rusty Bishop, and Calvin Porter for their field assistance, Dr. Duane Jeffery for reviewing the manuscript, Mark Rosenfeld for advice on karyotypic matters, and Sonya Tracy for darkroom assistance. Funding for this study was provided by the Associated Students of Brigham Young University, the Department of Zoology, and the Bean Endowment Fund of the M. L. Bean Life Science Museum.

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FOOD HABITS OF CLOUDED SALAMANDERS (*ANEIDES FERREUS*) IN CURRY COUNTY, OREGON (AMPHIBIA: CAUDATA: PLETHODONTIDAE)

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ABSTRACT.—Stomach contents of 650 clouded salamanders (*Aneides ferreus*), collected monthly throughout the year from Curry County, Oregon, were examined. Samples from three age classes were involved: (1) 489 adults, (2) 131 juveniles, and (3) 30 hatchlings. Foods did not vary by sex, but did vary by age and by season. Hatchlings ate small items, particularly mites, springtails, flies, and small beetles. Juveniles fed mainly on flies, isopods (sowbugs), beetles, mites, and centipedes in winter; beetles, ants, and isopods in spring; ants and beetles in summer; and isopods, beetles, and ants in fall. Adults ate isopods and beetles as their major foods in winter, spring, and fall and isopods, ants, beetles, and earwigs in summer. Four species were exceedingly important as foods for these salamanders: an unidentified isopod, the snout beetle (*Trachyphloeus bifoveatus*), the European earwig (*Forficula auricularia*), and an ant (*Lasius alienus*).

The clouded salamander (*Aneides ferreus*) is found from coastal northwestern California northward throughout western Oregon west of the Cascade Range to the Columbia River. Disjunct populations occur on Vancouver Island, British Columbia. In Oregon the clouded salamander is found from sea level to elevations of about 1525 m (Beatty 1979).

Aneides ferreus is associated with two basic types of habitat throughout its range—talus and fallen trees (Beatty 1979). Large fallen trees are the product of old-growth forests (Franklin et al. 1981, Harris et al. 1982). In Oregon the fallen tree habitat used by *A. ferreus* is essentially Douglas-fir (*Pseudotsuga menziesii*) in varying stages of decomposition (Beatty 1979, Maser and Trappe 1984, Phillips et al. 1981).

There have been few food-habit studies of *A. ferreus*. Fitch (1936) examined the stomach of five specimens from the Rogue River Valley in southwestern Oregon. Storm and Aller (1947) examined 63 stomachs from *A. ferreus* found in decaying Douglas-fir logs in western Oregon. Bury and Martin (1973) compared the distribution and foods of four species of plethodontid salamanders, including *A. ferreus*, from the redwood region of northern California; they examined 29 stomachs of this species.

Our study was undertaken to gain a more comprehensive idea of the food habits of *A. ferreus* throughout the year, by size groups, and by sex. All salamanders had been collected and preserved in connection with a previous study (Beatty 1979).

STUDY AREA

The study area, located 9.5 km south of the Pistol River, Curry County, Oregon, is in the Sitka spruce (*Picea sitchensis*) zone within the Klamath Mountains Province (Franklin and Dyrness 1973). The study area was burned in 1937 and 1938 and was salvage logged in the late 1950s and early 1960s. It has since been grazed continuously by domestic sheep (*Ovis aries*) (Fig. 1).

The area is open (low grass-forb vegetation with clumps of swordfern (*Polystichum munitum*) and trailing blackberry (*Rubus ursinus*) The widely scattered trees include Douglas-fir Sitka spruce, Pacific madrone (*Arbutus menziesii*), California laurel (*Umbellularia californica*), and clumps of red alder (*Alnus rubra*) Several large, charred Douglas-fir snags were still standing when the salamanders were collected (from 1974 through 1977), and the land was strewn with many large, fallen, decomposing, Douglas-fir trees. These trees composed the habitat of *A. ferreus* (Fig. 1).

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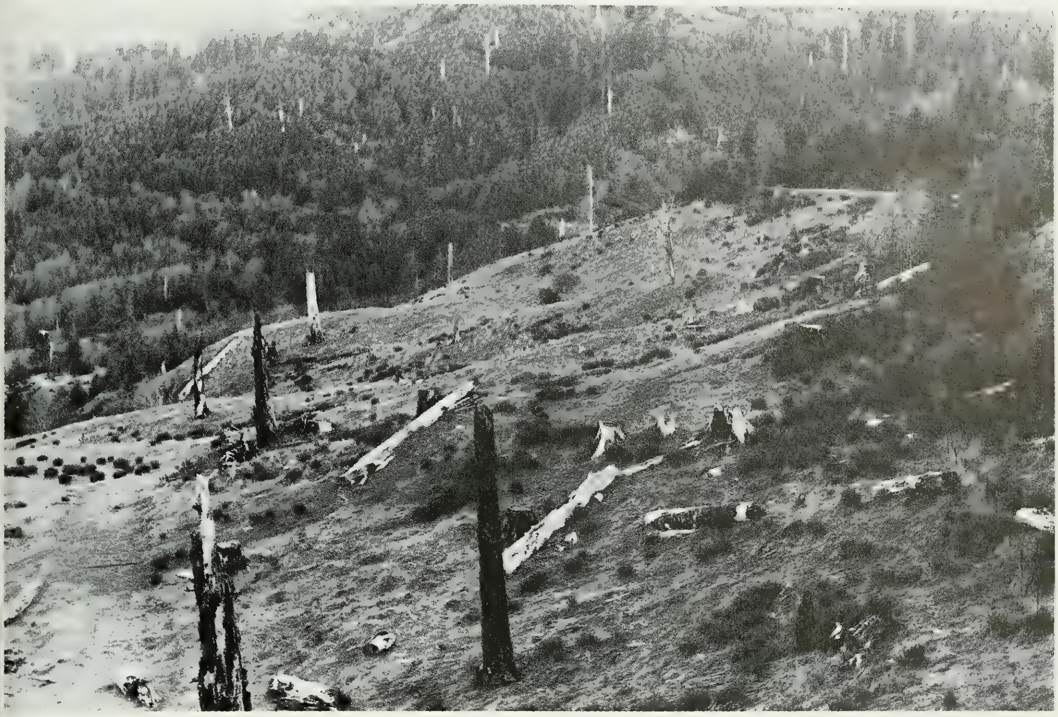

Fig. 1. Study area, 9.5 km south of the Pistol River, Curry County, Oregon. The large, woody materials formed the habitat of the clouded salamander.

Materials and Methods

The salamanders were collected by dissecting fallen trees and were placed in refrigerated containers to keep them cool and moist. They were transported to the laboratory within 24 hours (except the May sample), killed in 0.2% chlorobutanol, fixed in alcohol-formalin-acetic acid (AFA), washed in running tap water for 24 hours, and stored in 63% ethanol. Snout-vent length (SVL) was measured from the tip of the snout to the anterior edge of the cloaca.

The stomachs were opened later and the preserved food items were removed. Salamanders from every month of the year, except May, had food in their stomachs; the lack of food in specimens taken in May was probably the result of not preserving them soon enough after capture. Food items were examined in water with the aid of a 10-70 power zoom dissecting microscope. The food was identified as completely as possible, counted, and percent volumes visually calculated for each type of food in each stomach. Data were then summarized as mean percent volume, frequency of occurrence in stomachs, and percent frequency that each item composed of the total number of items. Data were separated by month, year, age class, and sex in the adult salamanders.

Results and Discussion

Results are given in Tables 1–6. To determine if there were any qualitative differences in feeding behaviors because of age, we separated the data into the following age classes: (1) adults (SVL > 45 mm), (2) juveniles (SVL 22–44 mm), and (3) hatchlings (SVL 14–19 mm).

Adults (SVL 45+ mm)

It appeared that foods of adult *A. ferreus* did not vary greatly by sex. To assess similarities and differences we used four of the larger individual samples: (1) 32 males, 54 females; 24 March 1976; (2) 15 males, 16 females; 11 April 1975; (3) 18 males, 13 females; 13 August 1976; (4) 15 males, 14 females; 30 November 1974.

Table 1. Food eaten in winter (December–February) by 55 adult *Aneides ferreus* (snout-vent length 45+ mm) from Curry County, Oregon.

Food item	Percent volume	Percent of individuals	Total percent volume for major group
Isopoda	44.0	39.4	(44.0)
Coleoptera			(22.9)
Curculionidae			(18.9)
Trachyphloeus bifoveatus	16.1	17.1	
Brachyrhinus rugosostriatus	1.8	0.6	
Chaetechus setiger	0.7	1.8	
Unidentified	0.3	0.6	
Carabidae			
Amara sp.	0.7	0.6	
Scarabaeidae			
Aphrodius cribratulus	2.6	1.8	
Unidentified adult	0.7	0.6	
Dermaptera			(5.9)
Forficula auricularia	10.8	5.9	
Diptera			(5.8)
Sciaridae	2.9	8.2	
Mycetophilidae	1.9	1.8	
Phoridae	0.1	0.6	
Unidentified larvae	0.9	1.2	
Araneida			(4.2)
Gnaphosidae	2.1	1.2	
Autrodiaetus pacificus	1.0	0.6	
Ebo sp. probably *pepinensis*	0.2	1.2	
Amaurobiidae	0.9	1.2	
Micryphantidae	0.04	0.6	
Chilopoda	1.8	0.6	(1.8)
Diplopoda	1.8	0.6	(1.8)
Homoptera			(0.7)
Aphididae	0.3	1.2	
Cercopidae	0.2	0.6	
Cicadellidae	0.2	0.6	
Hymenoptera			(0.7)
Formicidae			
Aphaenogaster subterraneus	0.6	1.8	
Lasius alienus	0.1	0.6	
Unidentified	0.04	0.6	
Neuroptera			(0.7)
Hemerobiidae	0.7	0.6	
Hemiptera			(0.3)
Tingidae	0.3	0.6	
Acarina	0.1	1.8	(0.1)
Collembola	0.04	3.5	(0.04)
Vegetation	3.3	—	
Unidentified insect	1.7	2.4	
Shed skin	1.1	—	
	100.0	99.9	

Percentages varied, perhaps because of small sample sizes. The preferred foods were identical in each case—sowbugs (isopods) ranked highest in three of the samples, but ants ranked highest in the 13 August sample. The next most abundant foods were snout beetles (curculionids) in the first two samples, isopods in the third sample, and beetles (coleopterans) in the fourth sample.

The number of sowbugs eaten by female salamanders was greater than the number eaten by males in three of the four samples; for example, females ate 23.8% more sowbugs in November than did the males. Spiders formed 16.1% by volume of the male diet in November but were absent from the female diet. In the August sample, spiders composed 11.5% by volume of the female salamander

TABLE 2. Foods eaten in spring (March–May) by 212 adult *Aneides ferreus* (snout-vent length 45+ mm) from Curry County, Oregon.

Food item	Percent volume	Percent of individuals	Total percent volume for major group
ISOPODA	61.4	41.7	(61.4)
COLEOPTERA			(19.8)
Curculionidae			(14.6)
Trachyphloeus bifoveatus	11.7	10.1	
Chaetechus setiger	2.1	2.0	
Rhyncolus sp.	0.6	0.4	
Brachyrhinus ovatus	0.2	0.1	
Carabidae			(3.0)
Calathus ruficollis	1.5	0.7	
Harpalus sp.	0.5	0.2	
Amara sp.	0.3	0.1	
Brachyrhinus rugosostriatus	0.3	0.2	
Unidentified	0.4	0.4	
Coccinellidae			
Soymnus ardelio	0.5	0.4	
Elateridae	0.2	0.1	
Byrrhidae			
Lioon simplicipes	0.1	0.1	
Tenebrionidae			
Tenebrio sp.	0.1	0.1	
Cucujidae	0.02	0.1	
Staphylinidae			
Tachyporus chrysomelinus	0.01	0.1	
Unidentified Coleoptera	1.0	1.8	
Unidentified larvae	0.3	0.1	
HYMENOPTERA			(5.2)
Formicidae			(5.0)
Lasius alienus	1.7	6.5	
Lasius pallitarsus	1.0	1.2	
Aphaenogaster subterraneus	0.7	3.2	
Tapinoma sessile	0.02	0.1	
Stenamma diecki	0.01	0.1	
Leptothorax sp.	0.01	0.1	
Unidentified	1.4	2.3	
Cynipoidea	0.1	0.2	
Vespidae	0.1	0.1	
DEMAPTERA			(5.0)
Forficula auricularia	5.0	5.5	
ARANEIDA			(3.7)
Linyphiidae	0.4	0.6	
Antrodiaetus pacificus	0.4	0.1	
Lycosidae	0.4	0.2	
Gnaphosidae	0.2	0.1	
Micryphantidae	0.1	0.1	
Mimetus hesperus	0.01	0.1	
Unidentified	2.2	1.5	
DIPTERA			(2.5)
Sciaridae	0.9	4.9	
Mycetophilidae	0.4	0.9	
Chironomidae	0.1	0.7	
Chironomid larvae	0.02	0.1	
Phoridae	0.02	0.1	
Dipterous larvae	0.1	0.2	
Unidentified	1.0	0.9	
ACARINA	0.11	4.7	(0.11)
CHILOPODA	0.6	0.6	(0.6)
LEPIDOPTERA			(0.3)
Larvae	0.2	0.1	
Adults	0.1	0.1	

Table 2 continued.

Food item	Percent volume	Percent of individuals	Total percent volume for major group
HOMOPTERA			(0.2)
Aphididae	0.2	0.2	
Cercopidae	0.04	0.1	
ORTHOPTERA			(0.2)
Gryllidae	0.2	0.1	
DIPLOPODA	0.1	0.2	(0.1)
HEMIPTERA			(0.1)
Tingidae	0.1	0.5	
COLLEMBOLA	0.06	3.3	(0.06)
Unidentified insects	0.4	0.7	
Vegetation	0.1	—	
	99.7	99.0	

TABLE 3. Foods eaten in summer (June–August) by 94 adult *Aneides ferreus* (snout-vent length 45+ mm) from Curry County, Oregon.

Food item	Percent volume	Percent of individuals	Total percent volume for major group
ISOPODA	25.3	8.9	(25.3)
HYMENOPTERA			(23.8)
Formicidae			(23.6)
Lasius alienus	15.2	55.5	
Tapinoma sessile	4.7	11.3	
Lasius pallitarsus	2.1	2.2	
Aphaenogaster subterraneus	1.3	0.5	
Leptothorax nitens	0.1	0.2	
Leptothorax crassipilis	0.1	0.2	
Leptothorax andrei	0.1	0.2	
Unidentified Hymenoptera	0.2	0.2	
COLEOPTERA			(22.4)
Curculionidae			(13.0)
Trachyphloeus bifoveatus	6.4	2.4	
Sitona hispidula	3.1	0.7	
Brachyrhinus rugosostriatus	1.9	0.7	
Rhyncolus sp.	1.2	0.3	
Chaetechus setiger	0.4	0.7	
Carabidae			
Calathus ruficollis	2.8	1.4	
Tenebrionidae			(2.0)
Helops sp.	1.1	0.2	
Phthora americanum	0.9	0.7	
Elateridae			
Ctenicera sp.	1.1	0.2	
Ostomidae			
Ostoma pippingskoldii	1.1	0.2	
Throscidae			
Pactopus hornii	0.6	0.2	
Staphylinidae			(0.5)
Quedius sp.	0.2	0.2	
Stenus sp.	0.1	0.2	
Byrrhidfae			
Lioon simplicipes	0.4	0.2	
Anobiidae			
Coelostethus quadrulus	0.3	0.2	

Table 3 continued.

Food item	Percent volume	Percent of individuals	Total percent volume for major group
Aleocharinae	0.1	0.2	
Atheta sp.	0.04	0.2	
Unidentified	0.02	0.2	
Cucujidae			
Pediacus depressus	0.1	0.2	
Scydmaenidae			
Lophioderus similis	0.1	0.2	
Unidentified	0.4	0.3	
DERMAPTERA			(11.9)
Forficula auricularia	11.9	4.1	
HOMOPTERA			(3.0)
Cercopidae	1.6	0.7	
Aphididae	0.02	0.2	
Unidentified	1.4	0.3	
LEPIDOPTERA			(2.9)
Larvae	2.3	1.0	
Adults	0.6	0.2	
ARANEIDA			(1.9)
Microphantidae	1.1	0.2	
Linyphiidae	0.6	0.3	
Ebo probably *pepinensis*	0.2	0.2	
CHILOPODA	1.8	0.5	(1.8)
HEMIPTERA			(1.6)
Lygaeidae	0.6	0.5	
Unidentified	1.0	0.3	
NEUROPTERA			(1.6)
Hemerobiidae	1.6	0.7	
DIPTERA			(0.7)
Sciaridae	0.02	0.2	
Unidentified larvae	0.6	0.5	
Unidentified	0.05	0.2	
PHALANGIDA	0.7	0.5	(0.7)
ORTHOPTERA			(0.6)
Gryllidae			
Gryllus sp.	0.6	0.2	
ISOPTERA			(0.4)
Holotermitidae			
Zootermopsis angusticollis	0.4	0.3	
NEMERTINEA	0.2	0.2	(0.2)
COLLEMBOLA	0.1	0.2	(0.1)
Vegetation	1.5	—	
	100.4	100.5	

diet but were absent from the stomachs of males. Thus, little or no preference for spiders was shown by either sex.

When the same four samples were combined, females were found to eat more sowbugs, curculionid beetles, and spiders than did males, but males did not eat appreciably more of any of the foods than did females. These data suggest that males use a greater diversity of foods. If this is true, then the total volume of these main foods should be greater in females than in males, but such a major difference (67.5% in males versus 81.5% in females) was only found in the August sample. Neither does such a trend show up when the number of food categories listed for each sex is examined. For example, 11 categories of foods were eaten by males and females in April and 15 by each sex in November. In August 22 categories were eaten by males and 12 by females; in March 24 categories were eaten by females and 14 by males. We combined the data for the sexes for seasonal comparisons because we detected no major differences in kinds of foods eaten by males versus females.

TABLE 4. Foods eaten in fall (September–November) by 125 adult *Aneides ferreus* (snout-vent length 45+ mm) from Curry County, Oregon.

Food item	Percent volume	Percent of individuals	Total percent volume for major group
ISOPODA	46.5	38.3	(46.5)
COLEOPTERA			(24.1)
Curculionidae			(16.0)
Trachyphloeus bifoveatus	13.8	12.0	
Chaetechus setiger	1.6	3.8	
Sitona hispidulus	0.2	0.1	
Unidentified	0.4	0.6	
Carabidae			(5.1)
Calathus ruficollis	4.5	1.8	
Unidentified	0.6	0.6	
Tenebrionidae			(0.9)
Phthora americanum	0.5	1.0	
Unidentified	0.4	0.1	
Scarabaeidae			(0.7)
Aphrodius sp.	0.7	0.6	
Staphylinidae			(0.3)
Atheta sp.	0.3	0.3	
Pselaphidae			(0.04)
Batrisodes sp.	0.04	0.1	
Unidentified	1.0	0.9	
Unidentified larvae	0.1	0.1	
HYMENOPTERA			(6.1)
Formicidae			(5.5)
Lasius alienus	2.1	9.0	
Aphaeonogaster subterranea	1.6	1.8	
Ant species #9	0.6	3.1	
Tapinoma sessile	0.5	1.6	
Camponotus vicinus	0.2	0.1	
Stenamma diecki	0.2	0.6	
Stenamma sp.	0.1	0.4	
Ant species #10	0.02	0.1	
Unidentified	0.2	0.7	
Vespidae	0.3	0.1	
Braconidae	0.1	0.1	
Unidentified	0.2	0.3	
DERMAPTERA			(4.6)
Forficula auricularia	4.6	1.2	
ARANEIDA			(4.3)
Clubionidae			
Trachelus californicus	0.4	0.3	
Gnaphosidae	0.4	0.1	
Linyphiidae	0.3	1.2	
Lycosidae	0.2	0.3	
Ebo probably *pepinensis*	0.1	0.1	
Micryphantidae	0.1	0.3	
Unidentified	2.8	1.0	
HEMIPTERA			(3.7)
Tingidae	1.4	1.5	
Lygaeidae	1.2	0.6	
Reduviidae	0.6	0.1	
Nabidae	0.5	0.3	
Unidentified	0.04	0.1	
LEPIDOPTERA			(1.6)
Adult	1.2	0.6	
Larvae	0.4	0.6	
HOMOPTERA			(1.5)
Cercopidae	1.1	1.0	
Aphididae	0.3	0.4	
Cicadellidae	0.1	0.1	

Table 4 continued.

Food item	Percent volume	Percent of individuals	Total percent volume for major group
DIPTERA			(1.4)
Tipulidae	0.9	0.9	
Sciaridae	0.04	0.1	
Mycetophilidae	0.04	0.1	
Dipterous larvae	0.1	0.3	
Unidentified	0.3	0.3	
ISOPTERA			(0.8)
Holotermitidae			
Zootermopsis augusticollis	0.8	3.5	
ORTHOPTERA			(0.4)
Gryllidae			
Gryllus sp.	0.4	0.1	
PHALANGIDA	0.4	0.6	(0.4)
ACARINA	0.3	2.4	(0.3)
NEUROPTERA			(0.3)
Hemerobiidae	0.2	0.3	
Larvae	0.1	0.1	
COLLEMBOLA	0.2	1.3	(0.2)
DIPLOPODA	0.1	0.1	(0.1)
Vegetation and debris	2.0	—	(2.0)
Unidentified insect	1.6	0.9	(1.6)
Unidentified insect larvae	0.04	0.1	(0.04)
	100.0	99.1	

WINTER.—We examined the stomachs of 55 adult salamanders taken during winter—December through February (Table 1). The major foods (by volume) were: (1) sowbugs, 44%; (2) beetles, 22.9% (primarily Curculionidae, 18.9%); (3) earwigs, 5.9%; (4) flies, 5.8%; and (5) spiders, 4.2%. Ants composed 0.7% of the total volume in the sample.

Three species were disproportionately important: (1) sowbugs 44.0%, (2) snout beetles (*Trachyphloeus bifoveolatus*) 16.1%, and (3) European earwigs (*Forficula auricularia*) 5.9%. The three species totaled 66.0% by volume of the total prey eaten. The same items occurred in 70.9%, 32.7%, and 16.4%, respectively, of the stomachs in the sample. They also composed 39.4%, 17.1%, and 5.9%, or a total of 62.4% of the total items eaten by the 55 salamanders. Although 33 kinds of food were eaten, the winter diet of *A. ferreus* in this locality was rather simple.

SPRING.—Stomachs of 212 salamanders were examined for spring diet—March through May (Table 2). Sowbugs were the major food, 61.4% by volume. Beetles, primarily curculionids, were second, 14.6% by volume. These items were followed by ants and earwigs, each composing 5.0%, and spiders, which accounted for 3.7% of the volume.

The three species (sowbug, snout beetle, and European earwig) that formed 66% of the winter diet, by volume, formed 78.1% of the spring diet—61.4%, 11.7%, and 5.0%, respectively, by volume. Sowbugs occurred in 80.7%, snout beetles in 28.3%, and earwigs in 9.9% of the stomachs, whereas the three composed 41.7%, 10.1%, and 5.5%, respectively, for a total of 57.3% of the items eaten.

Foods eaten in spring were relatively similar to those eaten in winter. The major difference was that flies decreased in use and ants increased.

SUMMER.—We studied the contents of 94 stomachs from salamanders collected from June through August (Table 3). Major differences in food habits among winter, spring, and summer were that in summer sowbugs and the snout beetles (*Trachyphloeus bifoveatus*) were much less important, even though beetles, as a whole, were about the same. Ants became an important food in summer and formed almost 25% of the diet. One ant (*Lasius alienus*), in fact, made up 55.5% of

TABLE 5. Foods of 131 juvenile *Aneides ferreus* (snout-vent length 20–45 mm from Curry County, Oregon. Presented as percent volume and percent of prey individuals.

	Winter		Spring		Summer		Fall	
Food item	Volume %	Individuals %	Volume %	Individuals %	Volume %	Individuals %	Volume %	Individuals %
ISOPODA	15.2	9.7	14.5	4.3	6.7	1.8	39.0	13.3
ACARINA	11.4	25.0	8.7	27.8	3.5	22.4	1.3	8.0
CHILOPODA	11.3	5.6						
COLLEMBOLA	5.5	23.6	4.4	22.2			3.8	44.4
COLEOPTERA								
Curculionidae								
Trachyphloeus bifoveatus	8.0	2.8	5.8	1.3	4.8	1.8	13.6	6.6
Chaetechus setiger			20.1	7.4				
Sitona hispidulus	0.4	1.4						
Rhyncolus sp.			0.5	0.4	1.3	0.6		
Carabidae								
Calathus ruficollis	1.0	1.4			1.2	0.6	1.9	0.3
Unidentified			2.4	0.4				
Coccinellidae								
Scymnus ardelio	4.0	1.4						
Staphylinidae								
Sitnao sp.			1.1	0.4				
Unidentified			2.3	1.3			0.5	0.3
Tenebrionidae								
Phthora americana							0.6	0.3
Byrrhidae								
Listemus formosus			1.1	0.4				
Pselaphidae			0.8	0.4	1.0	0.6		
Cucujidae					3.3	0.6		
Unidentified					3.3	0.6	1.4	1.0
Larvae					2.3	0.6		
HYMENOPTERA								
Formicidae								
Lasius alienus			1.3	1.3	24.3	38.2	9.2	5.6
Lasius pallitarsus			3.6	11.3	2.3	1.2		
Aphaenogaster subterranea			0.5	0.4	8.0	12.7		
Tapinoma sessile			0.3	0.4	9.5	7.3		
Stenamma diecki	4.4	2.8	0.5	0.4				
Unidentified	1.2	2.8	15.4	8.3	6.3	2.4	7.7	5.6
Unidentified							0.3	0.3
DIPTERA								
Sciaridae	4.0	4.2			2.5	1.2	0.1	0.3
Tipulidae	3.6	1.4						
Culicidae	0.4	1.4						
Phoridae			0.9	0.4				
Syrphidae					1.7	0.6		
Larvae	7.8	4.2					4.2	4.5
Unidentified	3.6	2.8	0.4	0.9				
LEPIDOPTERA								
Adult					1.8	0.6	1.2	0.3
Larvae							2.6	0.3
DERMAPTERA								
Forficula auricularia			1.4	0.9	0.7	0.6		
HOMOPTERA								
Cicadellidae			0.2	0.4	2.0	1.8	1.8	0.3
Cercopidae			0.9	2.2			0.1	0.3
Aphididae			0.9	2.2			0.1	0.3
Unidentified no results								
HEMIPTERA								
Lygaeidae	4.0	1.4			0.7	0.6		
Tingidae	3.8	2.8	1.6	0.4			0.8	1.4
Unidentified	0.8	1.4					0.5	0.3

Table 5 continued.

Food item	Winter Volume %	Winter Individuals %	Spring Volume %	Spring Individuals %	Summer Volume %	Summer Individuals %	Fall Volume %	Fall Individuals %
Neuroptera								
Hemerobiidae					3.3	0.6		
Araneida								
Linyphiidae	4.0	1.4						
Ebo pepinensis							0.6	0.7
Xysticus sp.							0.6	1.0
Unidentified			3.8	1.7	0.3	0.6	1.4	1.7
Phalangida							1.3	0.3
Diplopoda							0.5	0.7
Isoptera								
Holotermitidae								
Zootermopsis augusticollis			5.3	2.6				
Unidentified insect	5.6	2.8	1.6	1.3	2.7	0.6	0.5	0.7
Insect larvae			0.5	0.4			3.2	0.7
Vegetation and debris					4.3	—		
Shed skin							0.6	—
	100.0	100.3	99.9	99.6	99.8	99.8	100.1	99.5

all items eaten and 15.0% of the volume. Ants, as a whole, composed 70.2% of all organisms in the sample.

The three species that had been so important in winter and spring composed 43.6% of the summer diet: sowbugs, 25.3%; snout beetles, 6.4%; and European earwigs, 11.9%. There was nearly as great a diversity of foods represented in summer (52 categories) from a sample of 94 stomachs as in spring (55 categories) with a sample of 212 stomachs.

Fall.—We examined 125 salamander stomachs collected during fall—September through November (Table 4). Data for fall resembled those for spring. Major fall foods were sowbugs (46.5% by volume), beetles (24.1%, including 16.0% curculionids), ants (5.5%), European earwigs (4.6%), and spiders (4.3%). *Lasius alienus* was again the most important ant (61 individuals) and formed 2.1% of the volume and 9.0% of the total items in stomachs.

The three species that have been the most important foods, the sowbug, snout beetle, and European earwig, formed, respectively, 46.5%, 13.8%, and 4.6% of the volume, or 64.9% total volume; they also composed, respectively, 38.3%, 12.0%, and 1.2%, or a total of 51.5% of the organisms in the sample.

Annual.—The sowbug was the major food item of *A. ferreus* throughout the year, but it had its lowest relative use in summer. Beetles, collectively, and curculionid beetles in particular were clearly second by volume except in summer when ants were eaten in slightly greater amounts. European earwigs and/or ants were generally in third position by total volume. The earwigs were third in winter. Earwigs and ants were used about equally by volume in fall. Ants were second by volume in summer, followed by beetles, then earwigs, even though earwigs contributed their greatest volume (11.9%) during this time.

In terms of percent of prey individuals eaten, sowbugs, followed by beetles (mainly curculionids), were highest in winter, spring, and fall. The third and fourth most used food items were flies (11.8%) and earwigs (5.9%) in winter, ants (13.7%) and flies (7.9%) in spring, and ants (17.6%) and spiders (3.4%) in fall. Ants came first in summer; 70.0% of the organisms eaten were ants, followed by beetles (9.4%), sowbugs (8.9%), and earwigs (4.1%).

Juveniles (SVL 20–45 mm)

Winter.—The major foods of juveniles in winter (Table 5) were, in order of decreasing volume, flies (19.4%), sowbugs (15.2%), beetles (13.4%), mites (11.4%), centipedes (11.3%), hemipterans (8.6%), ants (5.6%), and

TABLE 6. Foods of 30 hatchling *Aneides ferreus* (snout-vent length 14–19 mm) from Curry County, Oregon.

	Fall (n = 17)			Winter (n = 13)		
	Volume %	Frequency %	Individuals %	Volume %	Frequency %	Individuals %
ACARINA	30.3	76.5	28.0	10.4	30.8	15.0
COLLEMBOLA	27.9	70.6	62.3	16.5	38.4	56.3
COLEOPTERA						
Trachyphloeus bifoveatus				5.8	7.7	1.3
Unidentified	14.7	35.3	3.4	7.7	7.7	3.8
HYMENOPTERA						
Formicidae	5.3	11.8	1.0	4.6	7.7	3.8
HOMOPTERA						
Cicadellidae				7.7	7.7	1.3
HEMIPTERA						
Tingidae	3.8	11.8	1.0			
DIPTERA						
Sciaridae				15.0	15.4	10.0
Chironomidae				7.7	7.7	1.3
Culicidae				3.8	15.4	3.8
Mycetophilidae				1.2	7.7	1.3
Larvae	4.4	17.6	2.9			
DIPLOPODA	2.9	5.9	0.5			
ARANEIDA	0.9	5.9	0.5	7.7	7.7	1.3
Insect larvae	5.9	5.9	0.5			
Unidentified insect				6.5	7.7	1.3
Unidentified material	3.8	17.6	—			
Vegetation				5.8	7.7	—
	99.9		100.1	100.4		100.5

springtails (5.5%). Thus, no foods were dominant. Rather, the important foods of hatchlings—flies, mites, and springtails—were still important but in lesser amounts, whereas some of the important foods of adults—sowbugs and snout beetles—were becoming important but much less so than in adults. This sample suggests a transition from foods of hatchlings to those of adults. The transition is apparently based on size of prey, from small to large, as a salamander grows.

SPRING.—By spring the juveniles could contend with larger prey items as follows, in decreasing volume: beetles (34.1%)—again primarily snout beetles; ants (21.6%); sowbugs (14.5%); mites (8.7%); termites (5.3%); and springtails (4.4%). There was considerable change from the foods eaten in winter. Flies, centipedes, and bugs decreased, and beetles and ants increased. The decrease in flies in the diet in spring, summer, and fall may be explained by availability. Flies are present and may be relatively inactive in fallen trees in winter, but in summer they either may not be present in large numbers or may be more active and caught less often. Ants may also be more abundant in spring, summer, and fall. Beetles are eaten more often, probably because the more mature salamanders have an easier time capturing them. We do not have a good explanation for the decrease in centipedes and bugs. These organisms only compose a major food source in winter, and even then only four centipedes and four bugs were involved, but each accounted for a large part of the respective stomach contents.

SUMMER.—The most important summer food was ants (50.4% by volume, 61.8% of the total prey). Ants were followed by beetles (17.2%), flies (4.2%), and mites (3.5%). No springtails occurred, and sowbugs—a major food in all other seasons—formed only 1.8% of the volume.

FALL.—The major items by volume were sowbugs (39.0%), beetles (18.0%), and ants (16.9%).

Many or most of the salamanders classified as juveniles have progressed past the size when the main foods were springtails, mites, and flies. This progress is best illustrated in a single collection of 38 subadult salamanders taken with full stomachs during 29–30 November 1974. Subadults separated nicely into two size classes: (1) 17 individuals with a snout-vent length of 14–18 mm, x̄ – 16.9, and (2) 21 individuals with a snout-vent length of 24–36 mm, x̄ = 29.3. Stomachs of hatchlings contained mites (30.3%) and springtails (27.9%); these two foods totaled 58.2% of the diet. Stomachs of juveniles contained only 7.0% springtails and 2.5% mites for a total of 9.5% for these two items.

Hatchlings (SVL 14–19 mm)

Among the smallest salamanders were six nestlings attended by both an adult male and female. The nest was found 13 September 1976. Five of the nestlings had stomachs that contained 100% yellowish material, thought to be yolk. The sixth had a stomach that contained three mites (5% by volume), an ant (*Tapinoma sessile*) (15%), a mycetophilid fly (30%), and a linyphyid spider (50%). Some feeding may therefore occur while the young are still in the nest.

With the exception of the above young and one collected in April, hatchlings (<20 mm SVL) were found from November through February. Of these, 17 were taken in fall and 13 in winter (Table 6). As expected, food items were small. Major foods in the fall sample, in order of decreasing volume, were mites, springtails, and very small beetles. These three groups composed 72.9% of the total volume. The mites and springtails occurred in about 70% to 75% of the stomachs, and the three together accounted for 93.7% of the prey items in the sample. No flies were found.

Small food items also dominated the winter sample. Springtails formed the most abundant prey items (56.3% of the total), but flies—primarily dark-winged fungus gnats, Sciaridae—made up the greatest collective volume (27.7%). In order of importance, by decreasing volume, were flies, springtails, very small beetles, mites, and spiders.

CONCLUSIONS

A newly hatched clouded salamander eats small food items (mites and springtails). As an individual matures, the size of prey increases to larger items, such as beetles and earwigs. All the prey listed in this paper can be found in and around large, fallen, decomposing Douglas-fir trees. Large, rotting Douglas-fir trees concentrate the salamanders' food; for example, some beetles and flies, eaten by the salamanders, depend on these trees for part or all of their life cycles (Deyrup 1975, 1976). Further, large, decomposing Douglas-fir trees remain moist inside during summer drought (Maser and Trappe 1984) and thereby maintain quality habitat not only for the clouded salamander but also for its food supply.

ACKNOWLEDGMENTS

D. Grayson, D. Metter, and J. Trappe critically read and improved this paper. D. Belnavis, H. Hanlin, W. Hoffman, S. Howe, and R. Pietruszka helped with the fieldwork. G. Peters, A. Moldenke, and J. Munsee identified some of the food items. B. Crook allowed us to collect the salamanders on his property. Fieldwork was supported by grants to JJB and RMS from the Theodore Roosevelt Memorial Fund, the American Museum of Natural History, and the Society of the Sigma Xi; identification of food items was supported by a grant to JOW from the USDA Forest Service, Pacific Northwest Research Station (Cooperative Agreement PNW-82-232). We are sincerely grateful for the help.

This paper represents a partial contribution (no. 3) of the project entitled "The Fallen Tree—An Extension of the Live Tree." The project is cooperative among the U.S. Department of the Interior, Bureau of Land Management; U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station; Oregon State University, Department of Forest Science; U.S. Department of Agriculture, Agricultural Research Service; and Oregon Department of Fish and Wildlife.

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WINTERING BATS OF THE UPPER SNAKE RIVER PLAIN: OCCURRENCE IN LAVA-TUBE CAVES

David L. Genter[1]

ABSTRACT.—Distribution and habitat selection of hibernating bats at the Idaho National Engineering Laboratory (INEL) and adjacent area are reported. Exploration of over 30 lava-tube caves revealed that two species, *Myotis leibii* and *Plecotus townsendii*, hibernate in the upper Snake River Plain. Five species, *M. lucifugus*, *M. evotis*, *Eptesicus fuscus*, *Lasionycteris noctivagans*, and *Lasiurus cinereus* are considered migratory. *Myotis leibii* and *P. townsendii* hibernate throughout much of the area, occasionally in mixed-species groups. *Myotis leibii* uses the dark and protected regions of the cave, usually wedged into tiny pockets and crevices near or at the highest portion of the ceiling. Individuals of *P. townsendii* may be found at any height or depth in the cave. Temperature appears to be the primary limiting factor in habitat selection. *Myotis leibii* was found in significantly cooler air temperatures than *P. townsendii*. Neither species tolerated continuous temperatures below 1.5 C. Relative humidity does not seem to be a significant factor in the distribution or habitat selection of the two species in lava-tube caves.

Field studies in the northern Rocky Mountains have provided fairly comprehensive records of bats for discontinuous geographic locations (Fenton et al. 1983, Genter 1985b, Negus and Findley 1959, Swenson and Shanks 1979). However, information regarding wintering species and their ecological requirements in the region is minimal.

An intensive survey of potential bat hibernacula, population size, and species composition was conducted during the winter of 1984–85 at the Idaho National Engineering Laboratory (INEL). Additionally, distribution and microhabitat preference of each species were investigated.

STUDY AREA AND METHODS

The INEL is on the upper Snake River Plain near the southeastern ends of the Lemhi and Lost River Mountain ranges. The elevation of this predominantly level plain averages 1,525 m. Two volcanic buttes near the southern boundary rise to 1,993 m. The vegetation is typical of the cold-desert in the Great Basin region. Recent basalt flows cover the southwestern portion of the site, extending throughout the adjacent Craters of the Moon National Monument (CROM). The northeastern area is a complex mixture of volcanic deposition, glacial debris, and Lake Terreton Playas. All caves studied were lava tubes restricted to the basalt flows (Fig. 1).

Temperatures were recorded with a Taylor bulb thermometer. Relative humidity was determined using a sling psychrometer (Taylor Instrument Co., Rochester, New York). Observations were made from 12 December 1984 to 27 January 1985, between 1000 and 1600 MST. Temperature and relative humidity were measured within each cave at the entrance and throughout the cave at approximately 15 m intervals regardless of the presence of bats and at sites where bats were hibernating. Voucher specimens are in the Zoological Museum of the University of Montana and in the vertebrate collection of the Radiological and Environmental Sciences Laboratory at the INEL.

RESULTS

Hibernating populations of *Myotis leibii* and *Plecotus townsendii* were found. Nine of the 31 caves investigated contained a total of 185 *P. townsendii* and 78 *M. leibii* (Table 1). Successive counts in each of several caves revealed that the number of individuals of each species remained constant within any cave. *Plecotus townsendii* were observed to move about within caves, but *M. leibii* apparently did not. Temperature within caves containing

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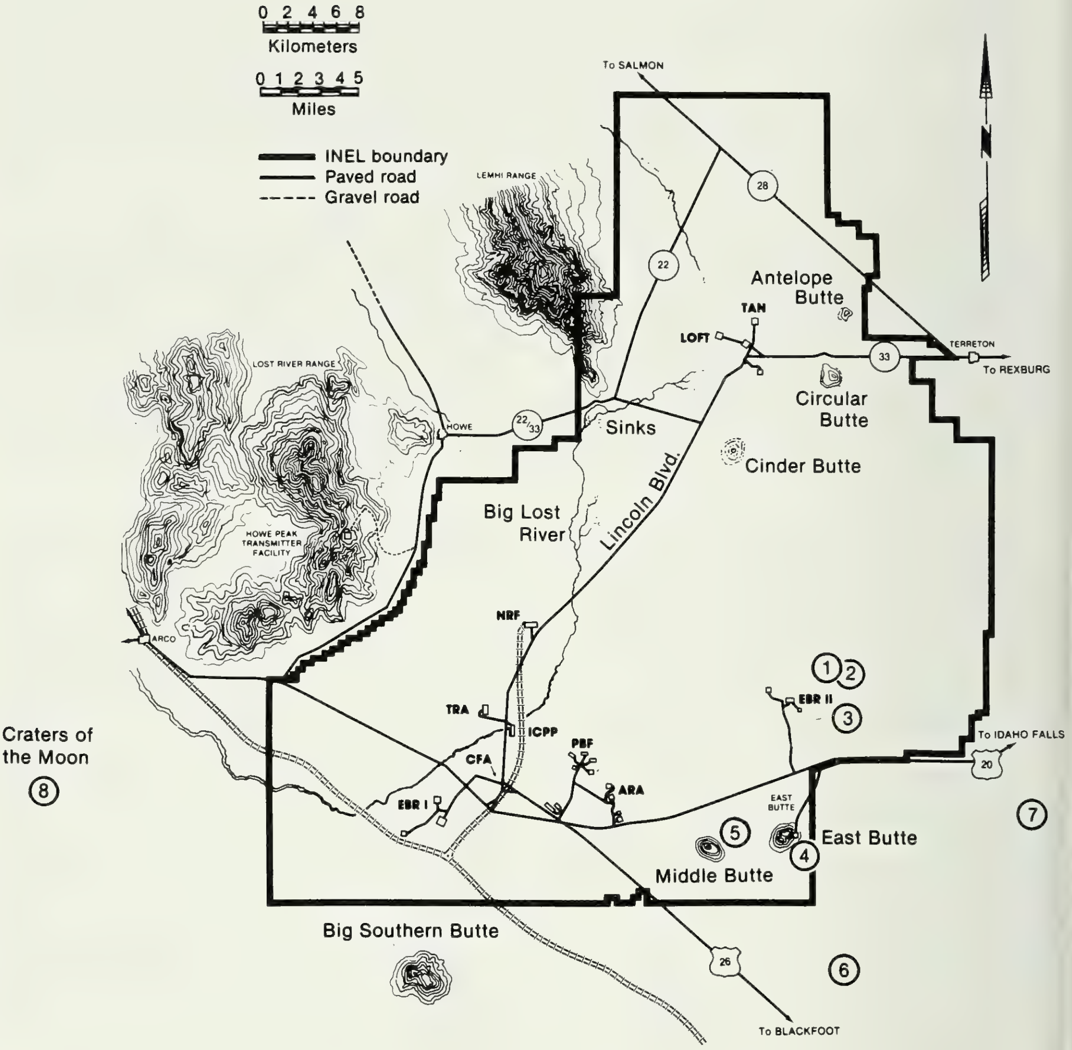
0 2 4 6 8
Kilometers
0 1 2 3 4 5
Miles
INEL boundary
Paved road
Gravel road
To SALMON
LEMHI RANGE
28
22
Antelope Butte
TAN
LOFT
TERRETON
33
To REXBURG
Circular Butte
LOST RIVER RANGE
HOWE
22/33
Sinks
Cinder Butte
Lincoln Blvd.
Big Lost River
HOWE PEAK TRANSMITTER FACILITY
ARCO
NRF
1
2
EBR II
3
TRA
ICPP
To IDAHO FALLS
Craters of the Moon
8
CFA
PBF
20
ARA
EBR I
EAST BUTTE
7
5
East Butte
4
Middle Butte
Big Southern Butte
26
6
To BLACKFOOT

Fig. 1. Bat hibernacula of the INEL basalt flow. 1, EBR II Cave 3. 2, EBR II Cave 4. 3, Rattlesnake Caves. 4, Moonshiner's Cave. 5, Middle Butte Cave. 6, Catscat Cave. 7, Sixteen Mile Cave. 8, Arco Tunnel.

bats ranged from −1.2 to 7.0 C. Temperatures of hibernacula were more limited. *Myotis leibii* was found in air temperatures from 1.5 to 5.5 C ($X = 2.4 \pm 0.82$). *Plecotus townsendii* inhabited significantly warmer regions of the caves ($t = 2.91$, $p < .05$), with temperatures ranging from 2.2 to 7.0 C ($X = 4.8 \pm 0.96$; see Table 1). Caves containing only *M. leibii* were colder overall than those containing only *P. townsendii* ($X = 1.8 \pm 1.38$ and $X = 4.7 \pm 0.51$, respectively; $t = 2.49$, $p < .05$). *Myotis leibii* would commonly be found in the warmer regions of cold caves (subfreezing), whereas *P. townsendii* was never found in caves with extensive areas of subfreezing temperatures.

Relative humidity varied widely among caves (< 43% to 100%). Hibernacula humidity ranged from 65% to 80% for *M. leibii* and from 68% to 100% for *P. townsendii* but was not significantly different between species ($t = 1.22$; $p > .1$).

Each species used different types of roosts within the caves. *Myotis leibii* was closely associated with textured and rimatious substrates. Eighty percent wedged themselves in crevices facing outward. All but 2 of the remaining 15 bats were in hollow depressions. In contrast, *P. townsendii* hung in exposed, open areas of the cave. *M. leibii* hibernated with the ventrum against the cave surface.

TABLE 1. Mean temperature and relative humidity with standard deviation for each cave. Number of each species counted with mean temperature for their roost sites.

Cave	Temperature (C)	Relative Humidity (%)	*Myotis leibii*	*Plecotus townsendii*
Arco Tunnel	0.9 ± 1.12	69.7 ± 5.3	3 (1.5)	0 (–)
Catscat Cave	2.0 ± 0.89	67.4 ± 11.3	4 (2.1)	0 (–)
Rattlesnake Cave (East Tunnel)	2.4 ± 0.82	78.4 ± 9.8	4 (2.4)	0 (–)
Rattlesnake Cave	3.9 ± 1.51	57.1 ± 12.9	41 (4.1)	132 (5.0)
Sixteen Mile Cave	4.2 ± 1.13	84.5 ± 4.7	16 (4.0)	8 (4.4)
Middle Butte Cave	4.7 ± 1.36	62.3 ± 14.7	9 (4.1)	15 (5.5)
EBR II - Cave 4	4.4 ± 0.59	80.3 ± 6.7	0 (–)	7 (4.7)
EBR II - Cave 3	4.8 ± 0.24	85.5 ± 7.5	0 (–)	11 (5.0)
Moonshiner's Cave	4.7 ± 0.49	100.0 ± 0.0	0 (–)	12 (4.8)

Plecotus townsendii hung from the substrate. In approximately 94% of the *P. townsendii* both ears were curled in a ram's horn fashion. The other 9 individuals had either one or both ears erect. All the latter were found in warmer (above 5 C) regions of the cave. Four bats with erect ears were fully aroused and occasionally took flight, whereas bats with curled ears never did so.

DISCUSSION

The length of time that a bat can hibernate has been estimated for several species (Studier and O'Farrell 1976, Hill and Smith 1984). In general, larger bats are capable of longer periods of hibernation and may undergo more frequent episodes of activity. Individuals of *M. leibii* were found in hibernacula with low air temperatures that varied little temporally or spatially. The narrow range of temperatures occupied illustrates habitat selection reflecting their need to conserve energy (McNab 1969, O'Farrell et al. 1971, Studier and O'Farrell 1976). Higher ambient temperatures induce a higher basal metabolic rate, and the ranges of temperatures chosen by bats keep them within species-specific energy budgets necessary for prolonged hibernation (Davis 1970, Hill and Smith 1984). The tendency of *M. leibii* to use crevices and sheltered areas likely subjected them to less environmental fluctuation.

Plecotus townsendii was the most abundant species found hibernating in the area. This may reflect a higher population density or lack of suitable wintering habitat for other species. *Plecotus townsendii* hangs from ceilings at varying heights and occupies nearly all depths within the caves. I did not observe them close to cave openings as did Twente (1955, 1960). Nearly all individuals of *P. townsendii* hibernated with their ears in ram's horn fashion, which may serve to decrease heat loss by radiation.

The apparent absence of other cavernous species of bats hibernating is not readily explained. Summer field studies indicated the few *M. lucifugus* at the INEL were closely associated with buildings. Nine individuals of *M. leibii* were recovered from within and around buildings late in September, suggesting these structures serve as hibernacula. *Eptesicus* left the caves used as summer roosts in late September. As is the case over much of its range, little is known on the wintering habits of *M. evotis*. Likely both *M. lucifugus* and *E. fuscus* winter in southeastern Idaho; these species commonly hibernate near their summer roost areas (Barbour and Davis 1969). Their absence in this study suggests that neither species finds lava-tube caves suitable for hibernation.

More extensive surveys are needed to gain a better understanding of the habitat selection and ecology of wintering bats in the northern Great Plains. Investigating a greater diversity of cavernous structures over a wider physiographic region should prove fruitful. The wintering ecology of bats is an important aspect of their life history and one that deserves further study.

ACKNOWLEDGMENTS

I thank L. H. Metzgar and O. D. Markham for reviewing a previous draft of this paper. This research was funded by the Office of

Health and Environmental Research, U.S. Department of Energy, and is a contribution of the INEL Radioecology and Ecology Program. Technical and logistical support were provided by many individuals at the Radiological and Environmental Sciences Laboratory at the INEL.

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GROWTH RATES OF MULE DEER FETUSES UNDER DIFFERENT WINTER CONDITIONS

Richard M. Bartmann[1]

ABSTRACT.—Based on forehead-rump length, growth rates of mule deer (*Odocoileus hemionus*) fetuses in Piceance Basin, Colorado, were slower during severe winters than during moderate ones. Growth rates in both situations were slower than reported for both mule deer and white-tailed deer (*Odocoileus virginianus*) fetuses from captive does.

Fetal forehead-rump measurements have displayed strong correlations with age in mule deer (*Odocoileus hemionus*) (Hudson and Browman 1959) and white-tailed deer (*O. virginianus*) (Cheatum and Morton 1946, Short 1970). These relationships were developed with captive deer maintained on artificial rations and provide no indication of variability that may occur in fetal growth rates under stress in natural environments. Verme (1963) reported slower fetal growth in captive white-tailed does in poor condition during the last third of gestation, and a possible relationship between poor doe condition and slower fetal growth was reported for white-tailed deer in New York (Jackson and Hesselton 1973).

The 1971 and 1972 winters in Piceance Basin, northwestern Colorado, were relatively moderate compared to harsh conditions in 1973, when an estimated 40% of the deer population perished (Bartmann and Bowden 1984). The severity of the latter winter allowed examining the effects of undue stress on fetal growth rates of mule deer.

STUDY AREA

Piceance Basin includes about 1,722 km^2 of pinyon-juniper (*Pinus edulis–Juniperus osteosperma*) winter range for mule deer at elevations between 1,675 and 2,285 m (Bartmann and Steinert 1981). Deer begin migrating to winter range in early October, with return migration to summer range in April and May. Deer movement across several major roads, particularly during late winter and spring, often results in a high incidence of road-killed deer.

METHODS

Fetuses were acquired from 83 mule deer does, aged 1$^1/_2$ to 10+ years, and included 58 road-kills, 18 trapping mortalities, 6 fence-kills, and 1 predator kill. Deaths occurred 25 March–13 May 1971 ($N = 13$), 21 January–14 April 1972 ($N = 19$), and 19 January–13 May 1973 ($N = 51$). Date of death was known for 54 does and known to within a maximum of two days for the remainder. Fetal data were taken only from does with the abdominal cavity intact and all fetuses undamaged. Forehead-rump measurements were made as described by Armstrong (1950). Measurements for twins were averaged to provide a single value.

Separate linear regressions of fetal forehead-rump length (mm) (Y) on collection date (Julian day) (X) were calculated for each year's data. Separate linear regressions were also calculated from data for known-age mule deer (Hudson and Browman 1959) and white-tailed deer (Cheatum and Morton 1946) fetuses 48–174 days old. Fetal ages in this study were estimated to be within this age range, and Short (1970) indicated a linear relationship adequately reflected this period of fetal growth.

Regression line slopes for Piceance deer were compared to those for known-age mule deer and white-tailed deer fetuses to test for differences in growth rates. I emphasize that the X variable in this study is collection date, whereas for the known-age fetuses it is fetal age. Collection date for a given deer can be written as age in days minus an unknown constant plus an error. If the population of deer fetuses was completely measured on a given

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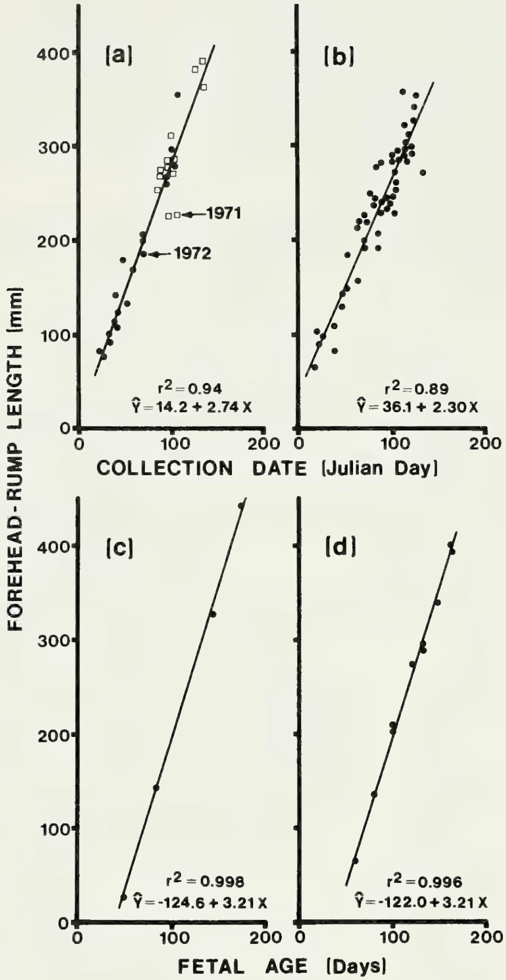

Fig. 1. Forehead-rump length as a function of collection date for mule deer fetuses collected in Piceance Basin, Colorado, January–May (a) 1971–1972 and (b) 1973. Forehead-rump length as a function of age for known-age (c) mule deer (Hudson and Browman 1959) and (d) white-tailed deer (Cheatum and Morton 1946) fetuses.

collection date, then the corresponding errors are assumed to have a mean of zero. Given the approach of Berkson (1950), the slope of the regression line of fetal length on collection date is then the same as the slope of the regression line of fetal length on age. Additional analyses were performed to test for differences in growth rates for single and twin fetuses and for size differences in male and female fetuses within the same twin set.

RESULTS AND DISCUSSION

Sample sizes for 1971 and 1972 were small compared to 1973, and fetal collections in 1971 occurred over only a $1\frac{1}{2}$-month period. Linear regression lines for these two years were similar (P = 0.91) (1971, Y = 3.1 + 2.81X; 1972, Y = 9.0 + 2.87X); but the line for 1972 was different (P = 0.02) from that for 1973. Since winter conditions in 1971 and 1972 were also similar, data from these two years were pooled and a new regression calculated.

The fetal growth rate in 1973 was slower (P = 0.02) than in 1971–1972 (Fig. 1a, 1b), and it wa also slower (P ≤ 0.002) than growth rates fo known-age mule deer and white-tailed deer fetuses (Fig. 1c, 1d). The rate in 1971–1972 wa also slower than the rate for known-age fetuses but differences were not quite significant (P ≥ 0.06).

Growth rates were similar (P = 0.87) for fetuses collected January–March (Y = 21.3 + 2.59X, N = 26) and April–May (Y = 10.7 + 2.50X, N = 25) in 1973. This suggests that i natural environments doe condition affects feta growth sooner than the last third of gestation a reported by Verme (1964).

Variability in fetal development due to sex an litter size is expected, but its effect on age-lengt relationships is unclear. Strong correlations between age and length of known-age mule dee and white-tailed deer fetuses (Fig. 1c, 1d) resulted despite not only small sample sizes (4 an 10, respectively) but also, with white-taile deer, a mix of single and twin fetuses of bot sexes. Differences in forehead-rump length of sets of mixed gender twins in this study range from 0–32 mm. Females averaged 3 mm long than males, but this difference was not signif cant (P = 0.09). In contrast, Jackson and Hesse ton (1973) found male fetuses were general larger than female fetuses at any given ag Growth rates for single and twin fetuses we compared separately for 1971–1972 and 197 Again, there was no difference (P ≥ 0.31) either case.

A common use of fetal growth rates is to est mate breeding dates. The growth rate for mu deer fetuses derived from data of Hudson ar Browman (1959) was applied to the 1971–19 and 1973 Piceance data. Linear regressions estimated breeding date on collection date we then calculated (Fig 2a, 2b). Both regression li slopes were >0 (P ≤ 0.001). Thus, the later

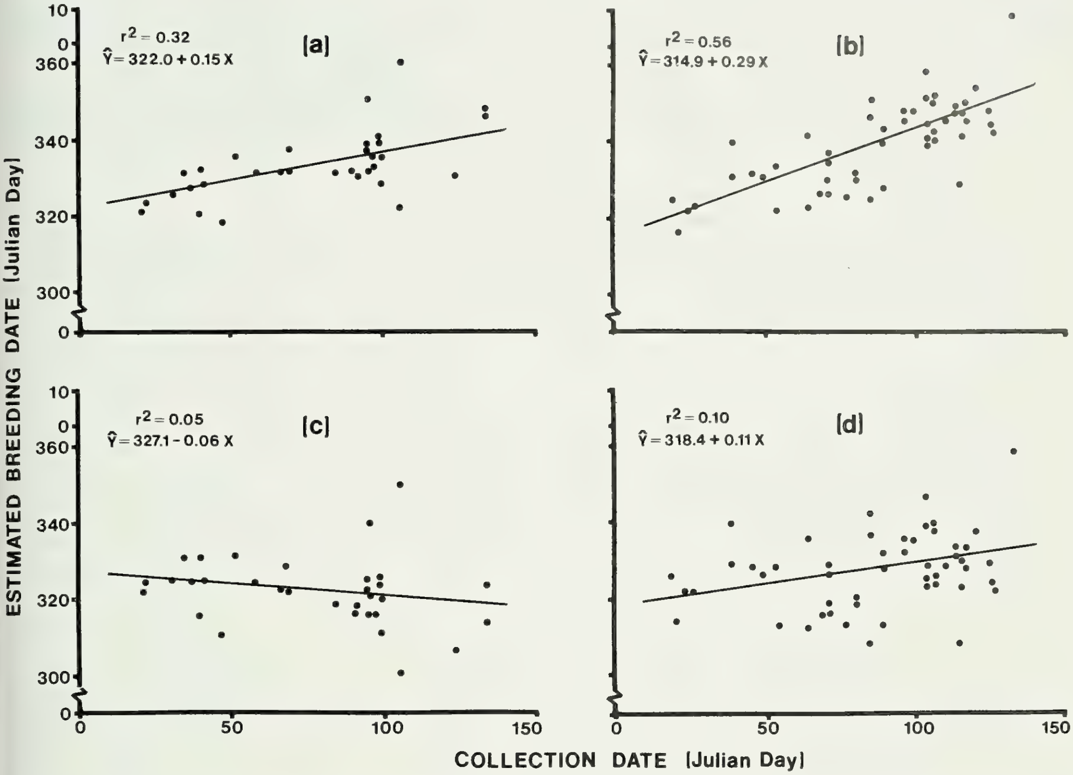

Fig. 2. Change in estimated breeding date with change in collection date of mule deer fetuses in Piceance Basin, Colorado, (a) 1971–1972 and (b) 1973 using the fetal growth rate calculated from data of Hudson and Browman (1959) and (c) 1971–1972 and (d) 1973 using the fetal growth rate of Thomas (1970).

gestation fetal data are collected, the later the breeding date estimate.

Thomas (1970) derived a fetal growth rate for Columbian black-tailed deer (*O. h. columbianus*) ($Y = 2.57X - 83.6$) based on fetuses from wild does plus known-age fetuses from two captives. This growth rate better characterized fetal growth in 1971–1972 because the regression line slope, although negative, was not different from 0 ($P = 0.23$) (Fig. 2c). However, slower fetal growth in 1973 still produced a slope >0 ($P = 0.02$) (Fig. 2d).

Results of this study indicated fetal growth can vary significantly with winter conditions, and published growth rates do not always fit wild populations. Thus, it is important that fetuses be obtained over the range of gestation to enable evaluating applicability of any fetal growth rate to be used.

ACKNOWLEDGMENTS

I thank D. C. Bowden, D. J. Freddy, N. T. Hobbs, F. B. Samson, and G. C. White for manuscript review and S. F. Steinert and J. J. Klein, Jr., for field assistance. D. C. Bowden also provided statistical assistance. Research was supported by Colorado Federal Aid to Wildlife Restoration Project W-38-R.

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DENNING HABITAT AND DIET OF THE SWIFT FOX IN WESTERN SOUTH DAKOTA

Daniel W. Uresk[1] and Jon C. Sharps[2]

ABSTRACT.—Swift fox (*Vulpes velox*) were investigated in western South Dakota to determine food habits and denning site characteristics. Over a three-year period food habits consisted of mammals (49%), followed by insects (27%), plants (13%), and birds (6%). Dens were located near hilltops within two habitat types, shortgrass and midgrass prairie; each type is characterized by differing plant species. Soil type was not a selective factor for den sites of swift fox. Management considerations for enhancing swift fox populations are presented.

The swift fox (*Vulpes velox*), a threatened species in South Dakota, was reported to be abundant on the Great Plains when settlers arrived (Egoscue 1979). With the increasing settlement of the northern High Plains, populations of swift fox declined, and by 1900 the species was rare in its northern range (Beck 1958, Soper 1964, Egoscue 1979). In South Dakota swift fox sightings were not reported between 1914 and 1966 (Hillman and Sharps 1978). The decline of the swift fox population has been attributed to the loss of natural prairie habitat, predator and rodent control programs, excessive trapping, and hunting (Egoscue 1979).

Since 1975 a small population of swift fox has been present in South Dakota, which provided an opportunity for observation of food habits and habitat characteristics around denning sites (Hillman and Sharps 1978). Other investigations on food habits and habitat of denning sites have been reported by Kilgore (1969) in Oklahoma and Cutter (1958a, 1958b) in Texas. However, very little information is available on swift fox food habits and den site characteristics within the northern range of its distribution.

The objectives of this study were to determine food habits of the swift fox and habitat characteristics at denning sites in western South Dakota.

STUDY AREA

The study areas selected were known to have viable swift fox populations. The first was located on the Pine Ridge Indian Reservation, Shannon County, South Dakota, approximately 23 km north of Oglala. This area is a broad flood plain with gently sloping to undulating upland prairie, bordered by the White River to the north. Badland outcroppings, which are found throughout the Pine Ridge area, are typified by bare soil; soil types are primarily clayey to sandy-clay-loam. Annual precipitation averages 41 cm, with an annual snowfall of 79 cm. Dominant vegetation consists of buffalograss (*Buchloe dactyloides*), needleleaf sedge (*Carex eleocharis*), blue grama (*Bouteloua gracilis*), and western wheatgrass (*Agropyron smithii*). Livestock graze throughout the area.

The second study area was located in Haakon County, 40 km north of Philip. This area is characterized by gently undulating hills with numerous livestock watering ponds. The soil type is primarily clay to clay-loam. Annual precipitation averages 43 cm, with an annual snowfall of 30 cm. Dominant vegetation of this area includes western wheatgrass, buffalograss, and blue grama. Livestock graze the area and, in addition, there is some farming.

METHODS

Swift fox were located by spotlighting within each of the study areas. On the Pine Ridge study site, three natal dens were studied during 1977 and 1978 and four in 1979. One natal den was studied north of Philip during 1978 and 1979.

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TABLE 1. Major plant species characterizing den sites of swift fox at two study areas (frequency of occurrence ≥ 5%) in South Dakota.

Species	% Frequency of occurrence	
	Pine Ridge	Philip
GRASS AND GRASSLIKE		
Western wheatgrass (*Agropyron smithii*)	32	87
Little bluestem (*Schizachyrium scoparium*)	11	
Red threeawn (*Aristida longiseta*)	13	
Blue grama (*Bouteloua gracilis*)	45	62
Japanese brome (*Bromus japonicus*)	6	
Cheatgrass brome (*Bromus tectorum*)	14	
Buffalograss (*Buchloe dactyloides*)	70	64
Sixweeks fescue (*Vulpia octoflora*)	8	
Needleandthread (*Stipa comata*)	24	5
Needleleaf sedge (*Carex eleocharis*)	46	25
FORBS		
Onion (*Allium* spp.)		12
Pinnate tansy mustard (*Descurania pinnata*)		13
Curlycup gumweed (*Grindelia squarrosa*)		20
Prairie sunflower (*Helianthus petiolaris*)		5
Stickseed (*Lappula redowskii*)		17
Prairie pepperweed (*Lepidium densiflorum*)		11
Virginia pepperweed (*Lepidium virginicum*)		25
Dotted gayfeather (*Liatris punctata*)		8
Rush skeletonplant (*Lygodesmia juncea*)	11	
Black medic (*Medicago lupilina*)		8
Yellow sweetclover (*Melilotus officinalis*)		13
Musineon (*Musineon divaricatum*)		5
Hoods phlox (*Phlox hoodii*)		7
Scarlet globemallow (*Sphaeralcea coccinea*)	19	10
Field pennycress (*Thlaspi arvense*)		9
Vetch (*Vicia* spp.)		6
SHRUBS		
Silky wormwood (*Artemisia* dracunculoides)	5	

Vegetation analyses were conducted during June and early September of 1978 and 1979. Frequency of occurrence was estimated along two 30m line transects located at each den site, and estimates were made by reading 30 2 × 5 dm quadrats systematically spaced at 1 m intervals along each of the transects (Daubenmire 1959). Data were summarized by transect and averaged over two years for both study areas. In addition, soils were measured at each den site for texture by the hydrometer method (Brady 1974).

Swift fox scats were collected weekly from adults and young pups at each den site from May through September of each year. Each collection consisted of 1 to 30 scats from each den site. Each sample was placed in a fine mesh nylon bag, washed in low-suds detergent, and rinsed. The bags and contents were then tumbled dry in a clothes dryer, which aided in separation of the prey material in the scats. The hair, feathers, bone, insects, plan material, and other items were used to identif prey remains in the scats (Johnson and Hanse 1977). Analyses of the scat materials were base on the 100-point frame method (Chamrad an Box 1964). Scat materials from the Philip are were combined with those from the Pine Ridg area because of small sample size. All frequenc of occurrence values were averaged for each yea and expressed as percent relative frequency b the following formula:

$$\text{Relative frequency} = \frac{\text{Frequency of occurrence of food item}}{\text{Total frequency of occurrence for all food items}} \times 10$$

Kulcynski's similarity index (Oosting 1956 compared swift fox diets among years. Spear man's rank-order correlation (r_s) and chi square contingency tables were used for die and vegetation analyses.

Table 2. Dietary composition (% relative frequency) of swift fox scats collected from two sites in South Dakota from May through September over a three-year period.

	Years			
Item	1977	1978	1979	Average
Mammals				
Sciuridae	43.3	25.5	18.5	29.1
Leporidae	4.9	7.0	0	4.0
Muridae (Cricitidae)	5.8	16.1	6.2	9.4
Heteromyidae	2.9	7.2	2.6	4.2
Geomyidae	0.5	3.1	0.6	1.4
Insectivora	0	0.6	0	0.2
Mustelidae	0	2.0	0	0.7
Bovidae	0	0.2	0	0.1
Birds	5.8	2.9	0.9	6.2
Insects	22.3	19.3	39.0	26.9
Plant	10.8	11.5	16.4	12.9
Other	4.3	4.4	6.8	5.2

RESULTS

Plants and Soils of Denning Sites

Vegetation associated with the denning sites of swift fox at Pine Ridge was much different than at the Philip site (Table 1). At Pine Ridge major grasses and grasslike plants in decreasing order included buffalograss, needleleaf sedge, blue grama, and western wheatgrass. A total of 17 grass and grasslike species was found on this area. Common forbs were scarlet globemallow (*Sphaeralcea coccinea*) and rush skeletonplant (*Lygodesmia juncea*). Thirty-nine forb species were recorded. The only shrub was silky wormword (*Artemisia dracunculoides*).

Vegetation associated with dens at Philip was less diverse than at Pine Ridge, with 43 and 57 species, respectively. However, the plants were more frequently represented at Philip (Table 1). Major grasses and grasslike plants were western wheatgrass, buffalograss, blue grama, and needle leaf sedge. A total of 10 grass species were observed. Forbs included 29 species with dominant ones being prairie pepperweed (*Lepidium virginicum*), curlycup gumweed (*Grindelia squarrosa*), stickseed (*Lappula redowskii*), and yellow sweetclover (*Melilotus officinalis*). The four shrub species present in the Philip area were silky wormwood, silver sagebrush (*A. cana*), sand sagebrush (*A. filifolia*), and fringed sagebrush (*A. frigida*).

Relative frequency of grasses and grasslike plants was 76% of the vegetation composition at Pine Ridge and 55% at Philip; however, forbs were lower, with 23% and 43% at Pine Ridge and Philip, respectively. Shrubs were low at both sites, with only 1% and 2% of the composition.

Soils were highly variable among denning sites. Soils at Pine Ridge were loam, clay-loam, and sandy-clay-loam. At Philip, soils were mostly clay.

Scat Analyses

The most frequent items in swift fox scats were mammals (49%), followed by insects (27%), plants (13%), and birds (6%) (Table 2). Swift fox dietary habits were different ($P < 0.05$) among the three years studied.

Average similarities varied among years when swift fox scat contents were compared. Scat contents for 1977 and 1978 were 54% similar. Scat contents were 72% similar between 1977 and 1979. However, 1978 and 1979 scats were only 41% similar in prey remains. This shows that food items were consumed in relatively different proportions among the years (Table 2).

Spearman's rank order correlations (r_s) among years were significant ($P < 0.01$), ranging from 0.76 to 0.89. This indicates that the food items found in the scats during the three years were consumed in same relative rankings.

The mammal species identified in the scats of swift fox included black-tailed prairie dog (*Cynomys ludovicianus*), hispid pocket mouse (*Perognathus hispidus*), northern pocket gopher (*Thomomys talpoides*), deer mouse (*Peromyscus maniculatus*), thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), northern grasshopper mouse (*Onychomys leucogaster*), western harvest mouse (*Reithrodontomys megalotis*), eastern cottontail (*Sylvilagus floridanus*), white-tailed jackrabbit (*Lepus townsendi*), voles (*Microtus* spp.), shrews (*Sorex* spp.), and undetermined Mustelidae. Cattle remains originating from carrion were also found in the scats.

Birds present in the scats included: Western Meadowlark (*Sturnella neglecta*), Chestnut-collared Longspur (*Calcarius ornatus*), Mourning Dove (*Zenaidura macroura*), Horned Larks (*Eremophila alpestris*), Lark Bunting (*Calamospiza melanocorys*), and Red-winged Blackbirds (*Agelaius phoeniceus*). Insects included were Orthoptera (grasshoppers) and Coleoptera (beetles). Plants included grass and cactus (*Opuntia* spp.) fruit.

DISCUSSION

Swift fox dens were generally located on or near the tops of hills on the undulating prairie in South Dakota, in pastures receiving moderate to heavy use by cattle. Cutter (1958a) reported on 25 dens in Texas, which were located within open sparsely vegetated areas on sloping plains, hilltops, or other well-drained areas; 19 of the dens found by Cutter were in heavily grazed pastures, and the 6 others in plowed fields and fence rows. In Oklahoma Kilgore (1969) found approximately 50% of swift fox dens in plowed fields and the others in shortgrass pastures. In our study swift fox dens were found in two habitat types, shortgrass and a midgrass prairie. Thus it has been shown that swift fox are able to select denning sites within various habitat types ranging from plowed fields, and fence rows, to a midgrass prairie having moderate livestock utilization.

Swift fox were not selecting dens within specific soil types in this study. Dens were located in four soil types in western South Dakota, and Kilgore (1969) also stated that dens were present on four soil types in Oklahoma. Most swift fox dens in our study were located near the tops of hills, which provides adequate drainage. Swift fox periodically clean their dens and pull soil from the den entrance, often in one direction indicating that the soil has a loose structure (Hillman and Sharps 1978). In our study dens were generally exposed in an easterly direction, and the natal dens had an average of four openings per den complex.

Prairie dogs, grasshoppers and beetles were the major components of the swift fox diet. Mammals provided 49% of the diet and insects 27%. In Texas Cutter (1958b) found that invertebrates provided 34% of the swift fox diet, while mammals provided 34%. Cottontails (*Sylvilagus* spp.) provided over 50% of the food consumed in the early spring by swift fox in Oklahoma (Kilgore 1969). Kilgore found that mammals, other than lagomorphs accounted for 82% of the fox diet during the autumn. Insects were also abundant in fox diets. Generally, from these studies and ours, it can be concluded that mammals and insects make up the major proportion of foods eaten by swift fox. Birds and plant material are less commonly consumed.

Human activities present the greatest threat to the swift fox in South Dakota (Hillman and Sharps 1978). Swift fox are easily trapped, shot, or poisoned and many times become victims of control efforts directed toward rodents and other predators. Predator and rodent control programs are being conducted which may impact swift fox in South Dakota. Bait treated with zinc phosphide has been used in western South Dakota and extensively on the Pine Ridge Indian Reservation for prairie dog control, but its use is reported to present only a minimal hazard to the swift fox (Schitoskey 1975). Compound 1080, developed for carnivores, has been released for predator and rodent control, which may result in poisoning of swift fox when application is within areas of swift fox residence. Compound 1080, used for prairie dog control, may have a secondary poisoning effect on the swift fox, since prairie dogs are a major component of the foxes' diet. To enhance the populations of swift fox, we need an accurate assessment of the swift fox distribution, especially on areas where predator and rodent control programs are being initiated. Our study shows that swift fox are not restricted to one habitat type, but several. An understanding of swift fox habitat requirements, i.e., food, water, cover, and tolerance to human disturbance, is essential to the successful management of the swift fox.

ACKNOWLEDGEMENTS

Special thanks is given to Conrad N. Hillman, who helped with the initial phases of this study. Credit is also given to Judy Johnson and Mike Whitcher for help with the field work and diet analyses.

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NEW TAXA AND COMBINATIONS IN THE UTAH FLORA

Stanley L. Welsh[1]

Abstract.— New taxa include: *Cryptantha cinerea* (Torr.) Cronq. var. *arenicola* Higgins & Welsh; *Physaria chambersii* Rollins var. *sobolifera* Welsh (Cruciferae); *Phacelia demissa* Gray var. *minor* N. D. Atwood (Hydrophyllaceae); *Iris pariensis* Welsh (Iridaceae); *Astragalus preussii* var. *cutleri* Barneby and *Pediomelum aromaticum* (Payson) Welsh var. *tuhyi* Welsh (Leguminosae); *Abronia nana* Wats. var. *harrisii* Welsh (Nyctaginaceae); *Camissonia atwoodii* Cronq. (Onagraceae); *Habenaria zothecina* Higgins & Welsh (Orchidaceae); *Aquilegia formosa* Fisch. in DC. var. *fosteri* Welsh (Ranunculaceae). New nomenclatural combinations include: *Rhus aromatica* Ait. var. *simplicifolia* (Greene) Cronq. (Anacardiaceae); *Lomatium kingii* (Wats.) Cronq., *L. kingii* var. *alpinum* (Wats.) Cronq. (Apiaceae); *Cryptantha cinerea* (Torr.) Cronq. var. *laxa* (Macbr.) Higgins; *Mertensia lanceolata* (Pursh) DC. var. *nivalis* (Wats.) Higgins (Boraginaceae); *Opuntia erinacea* Engelm. var. *aurea* (Baxter) Welsh (Cactaceae); *Arenaria fendleri* Gray var. *aculeata* (Wats.) Welsh, *A. fendleri* var. *eastwoodiae* (Rydb.) Welsh, *Lychnis apetala* L. var. *kingii* (Wats.) Welsh, *Stellaria longipes* Goldie var. *monantha* (Hulten) Welsh (Caryophyllaceae); *Draba densifolia* Nutt. ex T. & G. var. *apiculata* (C. L. Hitchc.) Welsh, *D. oligosperma* Hook. var. *juniperina* (Dorn) Welsh, *Physaria acutifolia* Rydb. var. *stylosa* (Rollins) Welsh, *Thelypodiopsis sagittata* (Nutt.) Schulz var. *ovalifolia* (Rydb.) Welsh (Cruciferae); *Lotus plebeius* (T. Brandg.) Barneby, *Lupinus polyphyllus* Lindl. in Edwards var. *ammophilus* (Greene) Barneby, *L. polyphyllus* var. *humicola* (A. Nels.) Barneby, *L. argenteus* Pursh var. *fulvomaculatus* (Payson) Barneby, *L. argenteus* var. *palmeri* (Wats.) Barneby, *Pediomelum aromaticum* (Payson) Welsh, *P. epipsilum* (Barneby) Welsh, *Psoralidium lanceolatum* (Pursh) Rydb. var. *stenophyllum* (Rydb.) Welsh, and *P. lanceolatum* var. *stenostachys* (Rydb.) Welsh (Leguminosae); *Mirabilis linearis* (Pursh) Hiemerl var. *decipiens* (Standl.) Welsh (Nyctaginaceae); *Camissonia boothii* var. *condensata* (Munz) Cronq., *C. boothii* var. *villosa* (Wats.) Cronq., *C. clavaeformis* (Torr. & Frem.) Raven var. *purpurascens* (Wats.) Cronq., *C. scapoidea* (T. & G.) var. *utahensis* (Raven) Welsh, *Oenothera caespitosa* var. *macroglottis* (Rydb.) Cronq., *Oe. caespitosa* var. *navajoensis* (Wagner, Stockhouse, & Klein) Cronq., *Oe. flava* (A. Nels.) Garrett var. *acutissima* (W. L. Wagner) Welsh, and *Oe. primiveris* Gray var. *bufonis* (Jones) Cronq. (Onagraceae); *Papaver radicatum* Rottb. var. *pygmaeum* (Rydb.) Welsh (Papaveraceae); *Dodecatheon pulchellum* (Raf.) Merr. var. *zionense* (Eastw.) Welsh (Primulaceae); *Aquilegia flavescens* Wats. var. *rubicunda* (Tidestr.) Welsh, *Delphinium andersonii* Gray var. *scaposum* (Greene) Welsh, *D. occidentalis* (Wats.) Wats. var. *barbeyi* (Huth) Welsh, and *Ranunculus andersonii* Gray var. *juniperinus* (Jones) Welsh (Ranunculaceae); *Purshia mexicana* (D. Don) Welsh and *P. mexicana* var. *stansburyi* (Torr.) Welsh (Rosaceae); *Galium mexicanum* H.B.K. var. *asperrimum* (Gray) Higgins & Welsh (Rubiaceae); *Castilleja parvula* Rydb. var. *revealii* (N. Holmgren) N. D. Atwood and *C. rhexifolia* Rydb. var. *sulphurea* (Rydb.) N. D. Atwood (Scrophulariaceae).

Nomenclatural changes are a bookkeeping chore that precedes the publication of most floras. The following changes of names and newly proposed taxa are published here prior to the publication of the Utah Flora, a work that has been in progress for some 25 years. The names published here are the products of the authors of the proposed taxa and nomenclatural combinations. Dr. N. Duane Atwood, Dr. Larry C. Higgins, Dr. Arthur Cronquist, and Dr. Rupert C. Barneby have kindly consented to having names and taxa currently in ongoing manuscripts published here so as to facilitate their use in the Utah Flora, which is nearing completion. The names are to be cited under the authorship of the person providing the combination, and are not to be cited as either "in" or "ex" Welsh. Each citation is considered as a separate proposal by the author of the constituent taxon or combination.

ANACARDIACEAE

***Rhus aromatica* Ait. var. *simplicifolia* (Greene) Cronq.** comb. nov. [based on Rhus canadensis var. simplicifolia Greene Bull. Torrey Bot Club 17: 13. 1890 (Greene sn., Peach Springs, Arizona, in 1889, at HDG!,may be presumed to be the holotype)].

APIACEAE

***Lomatium kingii* (Wats.) Cronq.** comb. nov. [based on: *Peucedanum graveolens*

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[1] Life Science Museum and Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

Wats. in King, Rep. Geol. Explor. 40th Parallel 5: 128. 1871; not Benth. & Hook. 1867. *Peucedanum kingii* Wats. Proc. Amer. Acad. Arts 22: 474. 1887 (Watson 463, Wahsatch and Uinta Mts.; holotype at US!; isotype at NY.!)].

***Lomatium kingii* (Wats.) Cronq. var. *alpinum* (Wats.) Cronq.** comb. nov. [based on: *Peucedanum graveolens* var. *alpinum* Wats. in King, Rep. Geol. Explor. 40th Parallel 5: 129. 1871. (Watson 464, East Humboldt Mts., Nev.; isotype at NY!)].

BORAGINACEAE

***Cryptantha cinerea* (Greene) Cronq. var. *arenicola* Higgins & Welsh** var. nov. Ab *Cryptantha cinerea* var. *abortiva* et al. in caule simplici et inflorescentia capitato vel subcapitato differt.

TYPE: USA: Utah. Kane Co. T41S, R5W, S26, Johnson Canyon, Lone Pine Point, at 1830 m, in Navajo blow-sand, in a pinyon-juniper, ponderosa pine, manzanita, and yucca community, 6 June 1984, L. C. Higgins, S. L. Welsh, & K. Thorne 14296 (Holotype BRY; 2 isotypes previously distributed as *C. cinerea*).

ADDITIONAL REPRESENTATIVE SPECIMENS: Utah. Kane County, ca 22 or 23 mi S of Alton, 27 May 1965, A. Cronquist 10191; ibid., Coral Pink Sand Dunes, 15 May 1984, N. D. Atwood 9636; ibid., 5 May 1966, S. L. Welsh 5299. Washington Co., Pocket Mesa, 8 June 1983, L. C. Higgins and A. H. Barnum 13615 (all BRY).

Much material of this taxon passed previously under the epithet *multicaulis*, a name that is synomymous with var. *jamesii*. The name provided above allows recognition of this distinctive phase of the species.

***Cryptantha cinerea* (Greene) Cronq. var. *laxa* (Macbr.) Higgins** comb. nov. [based on: *Oreocarya multicaulis* var. *laxa* Macbr. Contr. Gray Herb. 48: 35. 1916].

***Mertensia lanceolata* (Pursh) DC. var. *nivalis* (Wats.) Higgins** comb. nov. based on *Mertensia paniculata* var. *nivalis* Wats. Rep. Geol. Explor. 40th Parallel 5: 239. 1871].

CACTACEAE

***Opuntia erinacea* Engelm. var. *aurea* (Baxter) Welsh** comb. nov. [based on: *Opuntia aurea* Baxter Calif. Cactus 27, 28, 1933].

CARYOPHYLLACEAE

***Arenaria fendleri* Gray var. *aculeata* (Wats.) Welsh** stat. nov. [based on: *Arenaria aculeata* Wats. in King, Rep. U. S. Geol. Explor. 40th Parallel 5: 40. 1871].

***Arenaria fendleri* Gray var. *eastwoodiae* (Rydb.) Welsh** comb nov. [based on: *Arenaria eastwoodiae* Rydb. Bull. Torrey Bot. Club 31: 406. 1904, and the autonym var. *eastwoodiae* established by *A. eastwoodiae* var. *adenophora* Kearney & Peebles J. Washington Acad. 29: 475. 1939].

***Lychnis apetala* L. var. *kingii* (Wats.) Welsh** comb. nov. [based on: *Lychnis kingii* Wats. Proc. Amer. Acad. 12: 247. 1877].

***Stellaria longipes* Goldie var. *monantha* (Hulten) Welsh** comb nov. [based on: *Stellaria monantha* Hulten Bot. Notiser 1943: 265. 1943, and the autonym var. *monantha* established by *Stellaria monantha* var. *altocaulis* Hulten Bot. Notiser 1943: 267. 1943].

CRUCEFERAE

***Draba densifolia* Nutt. ex T. & G. var. *apiculata* (C. L. Hitchc.) Welsh** comb. nov. [based on: *Draba apiculata* C. L. Hitchc. Univ. Washington Publ. Biol. 11: 72. 1941, and the autonym var. *apiculata* established by *Draba apiculata* var. *daviesiae* (C. L. Hitchc. Univ. Washington Publ. Biol. 17 (2): 489. 1964].

***Draba oligosperma* Hook. var. *juniperina* (Dorn) Welsh** stat. nov. [based on: *Draba juniperina* Dorn Madrono 25: 101. 1978].

***Physaria acutifolia* Rydb. var. *stylosa* (Rollins) Welsh** stat. nov. [based on: *Physaria stylosa* Rollins, Contr. Gray Herb. 214: 14. 1984].

***Physaria chambersii* Rollins var. *sobolifera* Welsh** var. nov. A *Physaria chambersii* Rollins sensu stricto in caudicibus ramificantibus evolutis et foliis angustioribus et acutis differt.

TYPE: USA: Utah. Garfield Co., Escalante Mtns., head of Sweetwater Creek, above (east) of Widtsoe, bristlecone pine community on Wasatch Limestone Formation, 2 Aug. 1981, N. D. Atwood 8164 (Holotype BRY; Isotype, one distributed previously as *P. chambersii*).

ADDITIONAL SPECIMENS: Garfield Co., T34S, R1W, S22, center of S1/4, Dixie NF, Escalante Mtns., head of Escalante Canyon, 27.5 km 288 degrees from Escalante, 2,898 m, 60 degree slope, S exposure, with scattered Douglas-fir on raw, white, marl limestone, 20 June 1981, S. Goodrich 15666 (BRY); ibid., T35S, R4/2W, S22, Pink Wasatch Formation, at west end of Red Canyon, road to Bryce Canyon National Park, in ponderosa pine–limber pine community, 8 June 1982, Mutz and Zarnekee 82–70 (BRY).

This variety is partially sympatric with both varieties *chambersii* and *membranacea*, and the soboliferous condition might be an ecological response to creeping substrates. The recognition here calls attention of other workers to these plants and allows for further work.

Thelypodiopsis sagittata (Nutt.) Schulz var. *ovalifolia* (Rydb.) Welsh comb. nov. [based on: *Thelypodium ovalifolium* Rydb. Bull. Torrey Bot. Club 30: 253. 1903].

HYDROPHYLLACEAE

Material of *Phacelia demissa* Gray from the Uinta Basin differs subtly in several ways from that elsewhere in Utah. The plants are finely but not densely glandular-puberulent throughout, not densely glandular- villous to glandular puberulent; the corolla tube is bright yellow, not pale yellow; the sepals are fully twice as long as the capsule, not less than twice as long; the seeds are 4–12, not 10–16; and the plants average smaller. They are here designated as follows:

***Phacelia demissa* Gray var. *minor* N. D. Atwood** var. nov. Similis var. *demissae* in forma sed in pubescentibus, corollae tubis flavis, sepalis longioribus, seminibus paucioribus et minoribus differt.

TYPE: USA: Utah. Uintah Co., T3S, R23E, S4, ca 1.6 km E of Red Fleet Dam, at 1,891 m, in a desert shrub community, on clay hills, 31 May 1979, N. D. Atwood 7247 (Holotype BRY; isotypes 2, distributed previously as *Phacelia demissa* Gray).

ADDITIONAL REPRESENTATIVE SPECIMENS: Utah. Uintah Co., Uinta Basin, Utah Highway 121, 10.6 km east of Lapoint, T5S, R20E, S4, 1,675 m, abundant on gravelly hills, 25 May 1978, N. H. Holmgren, P. K. Holmgren, and R. C. Barneby 8758 (BRY); ibid., Orchard Creek, Dinosaur National Monument, Mancos Shale, Clay soil, Atriplex-Sarcobatus association, ca 1,455 m, 8 May 1955, S. L. Welsh 159 (BRY).

IRIDACEAE

***Iris pariensis* Welsh** sp. nov. Planta similis *Iride missouriensis* sensu latissimo sed in foliis angustioribus (2.5–5 mm nec 3–12 mm) bracteis suboppositis et angustioribus (2–3 mm nec 6–12 mm) et rhizomatibus gracilioribus (5–10 nec 10–20 mm) differt.

Rhizomes less than 10 mm thick, clothed with shredded fibrous leaf bases; leaves several to many on both fertile stems and innovations, 2–5 mm wide, (4) 7–24 cm long, stramineous to brownish or purplish basally; flower stem 4 cm tall, with several sheathing leaves free almost throughout; flower 1; spathaceous bracts linear-attenuate, 2–3 mm wide, 5–6 cm long, parallel, subopposite, herbaceous; ovary ca 12 mm long; perianth apparently white, the tube 15 mm long; sepals ca 6 cm long and 1 cm wide; petals narrowly oblanceolate, ca 6 cm long and 8 mm wide; style branches ca 2.8 cm long, the crests ca 7 mm long; anthers ca 13 mm long; capsule unknown.

TYPE: USA: Utah, Kane Co., T43S, R1E, East Clark Bench, south of US Highway 89, sandy soil, found in a semidesert grass shrub community at 1,403 m, May 1976, Vane O. Campbell 42 (Holotype BRY).

This distinctive narrow-leaved *Iris* species is compared to *I. missouriensis* in the diagnosis, but its relationships apparently lie with those far to the west in the coastal states. More material will provide both a better description and a better possibility of determining probable relationships.

LEGUMINOSAE

***Astragalus preussii* Gray var. *cutleri* Barneby,** var. nov., cum var. *preussii* legumine stipitato congruens sed ab ea statura pumila (caulibus 2–11 nec 10–40 cm altis) e radice annua ortis, foliolis paucis majusculis 5–11 et 12–20 x 7–12 mm usque, petalisque albidis pallide coerulescentibus (nec praeter alas saturate purpureis) diversa.

TYPE: U.S.A. Utah. San Juan Co.: common gravel outwash, Copper Canyon, 1 mi from mouth, 18 June 1938, Hugh C. Cutler 2283 (Holotype NY; isotypes, CAS, WIS); ibid., bench between Copper Canyon and No Man's Mesa, 22 May 1985, N. D. Atwood 11073 (Paratypes BRY, NY).

In my monograph (Mem. New York Bot. Gard. 13: 576. 1964) the type of var. *cutleri* was noticed as unusual in the species as represented in Utah Canyonlands for few and large leaflets but was passed over as a set of seedlings showing only juvenile foliage. The rediscovery by Duane Atwood of the same plant, found in a uniform population of small monocarpic individuals such as are never seen elsewhere in the range of var. *preussi*, show that I misjudged the significance of the differences. Moreover, the flowers were described by Cutler as varying from white to pale blue and by Atwood as white when fresh, acquiring a bluish keel-tip when dried. In southeastern Utah the petals of var. *preussii* are consistently vivid purple except for pallid wingtips. In the same region the leaflets of the longer leaves are at once more numerous (17–23) and smaller (6–15 x 3–6 mm) than those of var. *cutleri*. Leaves of allopatric var. *laxiflorus* Gray may be similar to those of var. *cutleri* in size and number, but its pod is sessile, its stems taller, and its range of dispersal different.

***Lotus plebeius* (T. Brandg.) Barneby** [based on: *Hosackia plebeia* T. Brandg., Proc. Calif. Acad. Sci. II, 2: 144. 1889 (Brandegee s.n. 30 Apr 1889, "El Rancho Viejo" [near Calmalli, Baja California Norte, +/- 28° 15' N]].

***Lupinus polyphyllus* Lindl. in Edwards var. *ammophilus* (Greene) Barneby** stat. nov. [based on: *Lupinus ammophilus* Greene Pittonia 4: 136. 1900].

***Lupinus polyphyllus* Lindl. in Edwards var. *humicola* (A. Nels.) Barneby** comb. nov. [based on: *Lupinus humicola* A. Nels. Bull. Torrey Bot. Club 25: 204. 1898].

***Lupinus argenteus* Pursh var. *fulvomaculatus* (Payson) Barneby** comb. nov. [based on: *Lupinus fulvomaculatus* Payson Bot. Gaz. (Crawfordsville) 60: 376. 1915].

***Lupinus argenteus* Pursh var. *palmeri* (Wats.) Barneby** stat. nov. [based on: *Lupinus palmeri* Wats. Proc. Amer. Acad. Arts 8: 530. 1873].

***Pediomelum aromaticum* (Payson) Welsh** comb. nov. [based on: *Psoralea aromatica* Payson Bot. Gaz. 60: 379. 1915, type from Bedrock Colorado, 17 June 1914, E. Payson 451 RM!].

***Pediomelum aromaticum* (Payson) Welsh var. *tuhyi* Welsh** var. nov. Ab *Pediomelum aromaticum* sensu stricto in floribus minoribus (6–7.3 mm nec 10–13 mm), calyce et dentibus minoribus (3.5–5.3 nec 10–11 mm et 1.6–2.9 mm nec 5–7 mm respecte), et caulibus decumbentibus differt.

TYPE: USA: Utah, San Juan Co., Rone Bailey Mesa, ca 17 km W of La Sal, T30S, R23E, S19, at 1,900 m, pinyon-juniper community, on mesa summit red siltstone of the Entrada Formation, 4 June 1985, S. L. Welsh & E. Neese 23500 (Holotype BRY, 4 isotypes to be distributed).

ADDITIONAL SPECIMENS: Utah, San Juan Co., T31S, R21E, S6, South Sixshooter Peak platform, Davis Canyon, at 1,708 m, on Moenkopi Formation in a shadscale community, 11 May 1982, S. L. Welsh, B. T. Welsh, and M. Chatterley 21092; ibid., Rone Bailey Mesa, 1 July 1984, J. S. Tuhy 1580; ibid., 4 June 1985, E. Neese & S. L. Welsh 16990; ibid., 19 June 1985, L. C. & E. Higgins 15812 (all BRY).

This phase of *P. aromaticum* is remote from the known populations near Bedrock, Colorado (the type locality), and in the Fisher Towers area vicinity east of Moab. The plants differ in subtle ways besides those cited in the diagnosis. When viewed from afar they appear grasslike in patches between sparse junipers on a rimrock situation atop Rone Bailey Mesa. The plants tend to sprawl, rather than stand erect as in the typical variety. The extensive rhizome system is similar, however, to the typical material. The variety is named in honor of its discoverer atop Rone Bailey Mesa, Mr. Joel Tuhy.

***Pediomelum epipsilum* (Barneby) Welsh** comb. nov. [based on: *Psoralea epipsila* Barneby Leafl. W. Bot. 3: 193. 1943, type from 17 mi E of Kanab toward Jepson Spring, 6 June 1942, Ripley & Barneby 4832 CAS!].

***Pediomelum pariense* (Welsh & Atwood) Welsh** comb. nov. [based on: *Psoralea pariensis* Welsh & Atwood Great Basin Nat. 35: 353. 1975, type from Bryce Canyon, 26 June 1975, S. L. Welsh & J. R. Murdock 12859 BRY!].

***Psoralidium lanceolatum* (Pursh) Rydb. var. *stenophyllum* (Rydb.) Welsh** comb. nov. [based on: *Psoralea stenophylla* Rydb. Bull. Torrey Club 40: 46. 1913].

***Psoralidium lanceolatum* (Pursh) Rydb. var. *stenostachys* (Rydb.) Welsh** comb. nov. [based on: *Psoralea stenostachys* Rydb. Bull. Torrey Club 40: 46. 1913].

NYCTAGINACEAE

Most specimens of *Abronia nana* Wats. are strictly acaulescent and have best developed leaves mainly less than twice as long as broad. These represent var. *nana*. However, in the San Rafael Swell, Emery County, Utah, there occur caulescent plants with main leaves 2–4 times longer than broad. These are named as follows:

***Abronia nana* Wats. var. *harrisii* Welsh** var. nov. Similis *Abroniae nanae* Wats var. *nanae* in anthocarpis floribus et bracteis sed in caulibus et foliis longioribus differt.

TYPE: USA: Utah. Emery Co., T20S, R11E, S22, San Rafael Swell, ca 1 mi S of San Rafael River campground, 1,586 m elev., Eriogonum- Astragalus-Hilaria community, 9 June 1979, J. Harris 364 (Holotype BRY; Isotypes, two distributed previously as *A. elliptica* A. Nels.).

ADDITIONAL SPECIMENS: Utah. Emery Co, T19S, R10E, S35, San Rafael Swell, on road to Wedge Overlook, ca 4 mi S of Buckhorn Flat crossroads, pinyon-juniper community, 13 June 1979, K. Despain 517 (BRY); do, T20S, R11E, S22, San Rafael Swell, Bottleneck Peak area, off the west side of Cottonwood Draw road, ca 2 mi S of Bridge Campground, 14 June 1979, K. Despain 564 (BRY). The plant is named after Dr. James Harris, student of the San Rafael Swell flora.

***Mirabilis linearis* (Pursh) Heimer var. *decipiens* (Standl.) Welsh** stat nov. [based on: *Allionia decipiens* Standl. N. Amer. Fl. 21: 223. 1918].

ONAGRACEAE

***Camissonia atwoodii* Cronq.** sp. nov. Species sectionis Chylismae; herba annua, glandulosa-puberula, rotusta, usque ad 15 dm alta, caule excurrenter ramosa, foliis leviter basin versus dispositis, laminis subrotundis, irregulariter denticulatis, 4–6 x 2.5–5 cm; inflorescentia terminalis, laxe ramosa, floribus pedicellatis, petalis purpureis 7–14 mm longis leviter versus axem dispositis, staminibus 4 + 4, inaequalibus, declinatis; fructus 12–25 mm longi, divaricato-deflexi, pedicellis divaricato-deflexis 3–5 mm longis, seminibus 1.5–8 mm longis, in quoque loculo biseriatis.

TYPE: USA: Utah. Kane Co., Smoky Creek Dugway, ca 17 mi NE of Glen Canyon City, Straight Cliffs Formation, 28 August 1973, N. D. Atwood 5957 (holotype NY!; isotype BRY!).

Robust, taprooted annual to 15 dm tall, with a single erect, excurrently branched stem; leaves scattered along the stem but somewhat basally disposed, at least some of the cauline ones evidently petiolate, with broadly ovate to ovate-oblong or elliptic, basally rounded to truncate or subcordate, irregularly denticulate blade 4–6 x 2.5–5 cm; herbage glandular-puberulent; flowers axillary to small bracts on the lateral branches and toward end of the main stem, in bud crowded, erect, and nearly sessile, but becoming more widely spaced and evidently pedicellate at anthesis, fairly showy and adapted to cross-pollination; petals purple, 7–14 mm long, somewhat asymmetrically (adaxially) disposed; stamens 4 + 4, unequal, declined; anthers ca 1.5–2 mm long; fruits 12–25 mm long, spreading-deflexed, on spreading-deflexed pedicels 3–5 mm long; seeds biseriate in each locule, plumply obovate from a substipitate base, 1.5–1.8 mm long, very finely cellular-reticulate.

This species is known only by several collections by Duane Atwood from the type locality on open slopes on the southwest side of the Kaiparowits Plateau, ca 27 km by road northeast of Glen Canyon City, Kane Co., Utah. Flowering is from August to October.

***Camissonia boothii* var. condensata (Munz) Cronq.** comb. nov. [based on: *Oenothera decorticans* var. *condensata* Munz Bot. Gaz. 85: 247. 1928].

***Camissonia boothii* var. *villosa* (Wats.) Cronq.** comb. nov. [based on: *Oenothera alyssoides* var. *villosa* Wats., Proc. Amer. Acad. Arts 8: 591. 1873; not *Oe. villosa* Thunb. 1794; typification will be discussed in the forthcoming treatment in the Intermountain Flora.].

***Camissonia clavaeformis* (Torr. & Frem.) Raven var. *purpurascens* (Wats.)** Cronq. comb. nov. [based on: *Oenothera scapoidea* var. *purpurascens* Wats. Proc. Amer. Acad. 8: 595. 1973].

***Camissonia scapoidea* (T. & G) Raven var. *utahensis* (Raven) Welsh** comb. nov. [based on: *Oenothera scapoidea* ssp. *utahensis* Raven Univ. California Publ. Bot. 34: 96. 1962].

Oenothera caespitosa **Nutt. var. *macroglottis*** **(Rydb.) Cronq.** stat. nov. [based on: *Pachylophus macroglottis* Rydb. Bull. Torrey Bot. Club 30: 259. 1903].

Oenothera caespitosa **Nutt. var. *navajoensis*** **(Wagner, Stockhouse, & Klein) Cronq.** stat. nov. [based on: *Oenothera caespitosa* ssp. *navajoensis* Wagner, Stockhouse, & Klein Monogr. Syst. Bot. Missouri Bot Gard. In press 1985].

Oenothera flava **(A. Nels.) Garrett var. *acutissima*** (W. L. Wagner) Welsh comb. nov. [based on: *Oe. acutissima* W. L. Wagner Syst. Bot. 6: 153. 1981, type from Flaming Gorge vicinity, Daggett County, Utah].

Oenothera primiveris **Gray var. *bufonis*** **(Jones) Cronq.** comb. nov. [based on: *Oe. bufonis* Jones, Contr. W. Bot. 8: 28. 1898].

ORCHIDACEAE

Habenaria zothecina **Higgins & Welsh** sp. nov. Planta *Habenaria sparsiflora* affinis et similis sed in calcari labium 1.5 longiore et floribus paucioribus differt.

TYPE: USA: Utah. Grand Co., ca 1.6 km N of Moab, T25S, R21E, S25, at ca 1,281 m, in a hanging garden community, 10 July 1985, S. L. Welsh & L. C. Higgins 23629 (Holotype BRY; 4 isotypes to be distributed.

ADDITIONAL COLLECTIONS: Utah. Grand Co., Arches National Monument, 28 Sept. 1963, S. L. Welsh & G. Moore 2735; ibid., Negro Bill Canyon vicinity, 3 August 1984, B. Franklin 1108. San Juan Co., Natural Bridges National Monument, 13 August 1963, S. L. Welsh & G. Moore 2410; ibid., 15 August 1963, S. L. Welsh & G. Moore 2503; ibid., The Neck vicinity, 31 Oct. 1964, S. L. Welsh & G. Moore 3840 (all BRY).

This peculiar, few-flowered bog orchid with its very long spurs has been known for many years. It has always been placed previously within an expanded version of *H. sparsiflora* but differs as outlined in the diagnosis and in other salient features. The leaves are broadly rounded initially, becoming obtuse and finally acute upward. The orchid grows in the vegetative assemblages known as hanging gardens along the canyons of the Colorado River in southeastern Utah. They occur there with maidenhair fern, sheathed death camus, and other shade-tolerant mesophytes. They occur mainly along the margin of the detrital slope adjacent to the back wall of the alcoves. Additional work is necessary to determine the total distribution.

PAPAVERACEAE

Papaver radicatum **Rottb. var. *pygmaeum*** **(Rydb.) Welsh** stat nov. [based on: *Papaver pygmaeum* Rydb. Bull. Torrey Bot Club 29: 159. 1902].

PRIMULACEAE

Dodecatheon pulchellum **(Raf.) Merr. var. *zionense*** **(Eastw.) Welsh** stat. nov. [based on: *Dodecatheon zionense* Eastw. Leafl. W. Bot. 2: 37. 1937, type from Zion Canyon].

RANUNCULACEAE

Aquilegia flavescens **Wats. var. *rubicunda*** **(Tidestr.) Welsh** stat. nov. [based on: *Aquilegia rubicunda* Tidestr. Amer. Midl. Nat. 1: 168. 1910].

A peculiar specimen of *Aquilegia* taken by Dr. Robert Foster from Zion Canyon in 1977 requires description. It has the habit and flower color of *A. formosa* but is glandular throughout and both petal spur and blade are longer than in that taxon. A search of the herbarium at Zion National Park yielded two specimens of the same taxon taken many years ago by Dr. Angus Woodbury. Initial efforts to relocate the area of collection of the type have been fruitless. There are many areas to be investigated, however, and the Hidden Canyon locality of the Woodbury specimens has not been searched recently. Possibly the specimens result from introgression between *A. formosa* and *A. chrysantha* Gray, both abundant in the canyon. The longer spurs and petal blades suggest such a possibility, but neither of the potential parents are glandular below the inflorescence. The plant is named after Dr. Robert Foster, enthusiastic collector and plant geographer.

Aquilegia formosa **Fisch. in DC. var. *fosteri*** **Welsh** var. nov. A var. *formosa* in petali laminis et calcari longioribus et herba glandulosis diversa.

TYPE: USA: Utah. Washington Co., T41S, R10W, S21, W of Tunnel, 1,373 m, N slope of

Bridge Mt., mountain brush community, on Wingate detritis, 25 May 1977, R. & R. Foster 3939 (Holotype BRY).

ADDITIONAL SPECIMENS: Utah. Washington Co., Zion National Park, Hidden Canyon, in 1924, A. Woodbury s.n. (ZNP herbarium, 2 specimens).

***Delphinium andersonii* Gray var. *scaposum* (Greene) Welsh** stat. nov. [based on: *Delphinium scaposum* Greene Bot. Gaz. 6: 156. 1881].

***Delphinium occidentalis* (Wats.) Wats. var. *barbeyi* (Huth) Welsh** comb. nov. [based on: *Delphinium exaltatum* var. *barbeyi* Huth Helios 10: 35. 1892].

***Ranunculus andersonii* Gray var. *juniperinus* (Jones) Welsh** stat. nov. [based on: *Ranunculus juniperinus* Jones Proc. Calif. Acad. II. 5: 616. 1895].

***Ranunculus acris* L. var. *aestivalis* (L. Benson) Welsh** comb. nov. [based on: *Ranunculus acriformis* var. *aestivalis* L. Benson Amer Midl. Naturalist 40: 43. 1948], type from 8.3 mi N of Panguitch].

ROSACEAE

***Purshia mexicana* (D. Don) Welsh** comb. nov. [based on: *Cowania mexicana* D. Don Trans. Linnaean Soc. 14: 575. 1825].

***Purshia mexicana* (D. Don) Welsh var. *stansburyi* (Torr.) Welsh** stat. nov. [based on: *Cowania stansburiana* Torr. in Stansbury Expl. Surv. Utah 386. 1852].

RUBIACEAE

***Galium mexicanum* H.B.K. var. *asperrimum* (Gray) Higgins & Welsh** stat. nov. [based on: *Galium asperrimum* Gray Mem. Amer. Acad. Arts II. 4: 60. 1849].

SCROPHULARIACEAE

***Castilleja parvula* Rydb. var. *revealii* (N. Holmgren) N. D. Atwood** stat. nov. [based on: *Castilleja revealii* N. Holmgren Bull. Torrey Bot. Club 100: 87. 1973].

***Castilleja rhexifolia* Rydb. var. *sulphurea* (Rydb.) N. D. Atwood** stat. nov. Based on: *Castilleja sulphurea* Rydb. Mem. New York Bot. Gard. 1: 359. 1900].

NEW TAXA IN MISCELLANEOUS FAMILIES FROM UTAH

Stanley L. Welsh[1]

Abstract.—Named are the following: *Astragalus limnocharis* Barneby var. *tabulaeus* Welsh var. nov., from the pass between Boulder Mountain and the Table Cliff Plateau, Garfield County, Utah; *A. eremiticus* Sheldon var. *ampularioides* Welsh var. nov. from Washington County, Utah; *Lupinus argenteus* Pursh var. *moabensis* Welsh var. nov., from southeastern Utah, validated by inclusion of a Latin diagnosis; *Erigeron zothecinus* Welsh sp. nov. described from moist alcoves along Lake Powell, eastern Kane County, Utah; *Cleomella palmerana* Jones var. *goodrichii* Welsh var. nov. described from Uintah County, Utah; *Arabis vivariensis* Welsh sp. nov. named from northeastern Uintah County, Utah; *Draba kassii* Welsh sp. nov. described from material taken in the Deep Creek Mountains, western Tooele County, Utah.

A curious, small-flowered *Astragalus* was discovered by Sherel Goodrich and me immediately north of the pass between Boulder Mountain and Table Cliff Plateau 20 June 1981. The material was first taken to be an extension of the similar *A. montii* Welsh from much farther north on the Wasatch Plateau, primarily on the basis of the pink-purple flowers. However, the wing tips are not white, and the flowers average smaller than in that taxon. Placement with the geographically nearer and morphologically more similar *A. limnocharis* Barneby became evident with additional study. The flower size, shape of petals, and pod size and conformation fit well within the range for *A. limnocharis*. The strongly soboliferous habit and pink-purple flowers are notably different, however. The soboliferous habit is an adaptation that allows occupation of the steep slopes where the plants grow, a habitat not usually occupied by *A. limnocharis* proper. The presence of sobols might represent merely an ecological response to the creeping mantle on the slopes, but it is readily apparent both in the field and in herbarium specimens.

The plants from adjacent to the Table Cliff Plateau are named as follows:

***Astragalus limnocharis* Barneby var. *tabulaeus* Welsh** var. nov. Planta persimilis *Astragalo limnochari* Barneby in floribus et fructus sed in caudicibus soboliferis et floribus purpureis differt.

Type: USA: Utah. Garfield Co., T34S, R1W, SE/SW S22, ca 2,930 m in a *Pinus longaeva* community, on the White Limestone Member of the Wasatch Formation, on a 60%–70% south-facing slope, 20 June 1981, S. L. Welsh 20666 (Holotype BRY; 2 isotypes distributed previously as *A. montii*).

Additional specimens: Utah. Garfield Co., same approximate locality and date as the holotype, S. L. Welsh 20667, 20667a, and S. Goodrich 15662, 15669 (all BRY).

Growing on the Chinle Formation west of the Gunlock intersection at Shem, Washington County, Utah, is a second more or less distinctive phase of *Astragalus eremiticus* Sheldon. The plants simulate *A. ampullarius* in having subterranean caudices and short, broad, long-stipitate pods. The pods are smaller than in *A. ampullarius*, but the stems recline as in that species. The elongate many-flowered racemes are similar to those of typical *A. eremiticus*, which occurs elsewhere in the county, but the flowers are more numerous (up to 45), the peduncles more elongate (up to 21 cm), the raceme very lax in fruit (up to 25 cm), and the pods are tumid and truncate to obtuse basally and 8-15 (18) mm long and 6-12 mm wide. Pods of some plants from elsewhere in Washington County are tumid but not as abruptly broadened or as broad as in the Shivwits plants. And, when the pods are tumid, the other features are as in typical *E. eremiticus*. The habitat consists of barren silty clays of the Chinle Formation, a stratum supporting *A. ampullarius* in all its known localities. Because of the similarities to *A. ampullarius*, this distinctive phase is designated as follows:

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***Astragalus eremiticus* Sheldon var. *ampullarioides* Welsh** var. nov. Planta similis *A. eremitico* var. *eremitico* in racemis et floribus sed in leguminibus brevioribus et latioribus et caudicibus subterraneis differt, et similis *A. ampullario* in leguminibus formis et caudicibus subterraneis sed in racemis elongatis et floribus plus numerosis et coloris flavis differt.

TYPE: USA: Utah. Washington Co., T41S, R17W, N of Highway 91 at Shivwits, 1050 m elev., 21 Apr. 1982, S. L. Welsh and N. D. Atwood 21049 (Holotype BRY; an isotype distributed previously as *A. eremiticus* Sheld.).

ADDITIONAL SPECIMENS: Utah. Washington Co., ibid., 4 May 1976, N. D. Atwood 6586 (BRY); ibid., 9 June 1983, L. C. Higgins and N. D. Atwood 13683 (BRY); ibid., May 1985, S. L. Welsh 23456 (BRY).

The plants are evidently relished by livestock, and in most years the inflorescences are eaten. The extent of the population is unknown.

The presumption was made by Welsh (1978, p. 326) that a name proposed by Dunn and Harmon for the large flowered phase of *Lupinus argenteus* in southeastern Utah had been or was about to be effectively and validly published. That name, it turns out, was never published by Dunn and Harmon and was effectively but not validly published as a nomen nudum by Welsh. To correct that imperfection the name is here published with a Latin diagnosis:

***Lupinus argenteus* var. *moabensis* Welsh** var. nov. [*L. argenteus* var. *moabensis* Welsh, nom. nud.; *L. argenteus* ssp. *moabensis* Dunn & Harmon ex Welsh, nom. nud.]. A var. *argenteo* caeterius persimili floribus maximus, alis 12-14 (nec 8-12) mm longis differt.

TYPE: USA: Utah. Grand Co.: Professor Valley Ranch, T24S, R23E, S27, 1,342 m elev., sandy soil, 28 April 1977, S. L. Welsh and K. Taylor (Mastin) 14632 (Holotype BRY; Isotype NY, and 8 others distributed previously).

ADDITIONAL SPECIMENS: Utah. Grand Co., 5 km W of Deadhorse Point, 26 May 1950, W. P. Cottam 12107; ibid., 2 km S of Landscape Arch, 19 May 1949, B. F. Harrison 11414; ibid., 3 June 1963, S. L. Welsh & G. Moore 2028; ibid, Between Moab and Castleton on the Colorado River, 13 May 1933, W. P. Cottam 5620; ibid., T25S, R24E, S29, Castle Valley, 18 May 1982, S. L. & E. R. Welsh 21154; ibid., T24S, R23E, S26, Professor Valley Ranch, S. L. Welsh & K. Taylor (Mastin) 14631; ibid., T25S, R23E, S9, ca 1 km east of Castle Rock, 28 Apr. 1984, S. L. Welsh & D. Trotter 22719. Emery Co., T22S, R8E, S6, ca 15 km E of Emery, 13 May 1981, S. L. Welsh 20462; ibid., T24S, R9E, S18, San Rafael Swell, 22 May 1980, J. G. Harris 731; ibid., Rock Springs Bench, NE of Cathedral Valley Jct., 10 June 1973, H. K. Harrison 1026. San Juan Co., Road to Upheaval Dome, Island in the Sky, 9 July 1964, G. Moore 200, 213; ibid., Island in the Sky, 16 May 1965, G. Moore 392 (all BRY).

This is the early flowering, large flowered phase of *L. argenteus* that occurs at low elevations, mainly along sandy washes in mixed and warm desert shrub communities.

During a study of hanging gardens in the Glen Canyon National Recreation Area, a curious daisy was discovered in a moist alcove near the confluence of Glen Canyon and Escalante Canyon. The seepy alcove faces to the south and extends along a horizontal bedding plane for several hundred feet, forming a series of minor alcoves. Traditional hanging garden plants, such as *Primula specuicola*, are present in the garden community. The daisy occurred within the hanging garden assemblage mainly at the base of the face wall, where some detritis has accumulated. Only a few species of the enormous genus *Erigeron* occur in this habitat in Utah. This one seems to be specialized for growth in the moist, evidently saline substrate that is constantly renewed by addition of sand from the alcove face. It is similar in size of flower heads and general aspect with *Erigeron abajoensis* Cronq., a species of montane sites in southern Utah. The alcove daisy differs from its montane counterpart in having linear to narrowly oblanceolate basal and cauline leaves, fewer pappus bristles, and glands in addition to strigose to spreading stiff hairs on the involucral bracts. The species is named and described as follows.

***Erigeron zothecinus* Welsh** sp. nov. Planta similis *Erigeronte abajoensi* Cronq. in capitulis et bracteis sed in foliis angustioribus, pappo paucioribus, et bracteis glandulosis differt.

TYPE: USA: Utah. Kane Co., T40S, R91/2E, S36, GCNRA, Lake Powell, N Escalante hanging gardens, ca 1,140 m elev., Navajo Sandstone, 29 May 1983, S. L. Welsh 22115 (Holotype BRY; 5 isotypes to be distributed).

ADDITIONAL SPECIMENS: Utah. Kane Co., same locations as the type, 29 May 1983, S. L. Welsh 22128; ibid, 24 May 1984, S. L. Welsh 22860, both BRY.

In 1979 Sherel Goodrich discovered a population of *Cleomella palmerana* Jones north of Split Mountain in Uintah County, Utah. The material was routinely assigned to the species as it was understood in eastern Utah. However, the habit of growth and fruit characters differ from the body of the species. The raceme stands above the foliage, and the fruit is distinctly horned, resulting in fruit 8-9 mm wide, not 3-5 mm wide as in the material from south of the Uinta Basin. Because of these differences the plants are here designated as follows:

***Cleomella palmerana* Jones var. *goodrichii* Welsh** var. nov. Ab. *Cleomella palmerana* var. *palmerana* in fructu latioribus et cornuto differt, et similis *Cleomella plocasperma* Wats. in fructu ambitu sed in foliis latioribus differt.

TYPE: USA: Uintah Co., T3S, R24E, S25, Rainbow Draw, 1,647 m elev, Morrison Formation, eroded slopes of heavy raw, vertisol-like clay, soil violently effervescent with 10% HCl, with *Machaeranthera venusta*, *Phacelia demissa*, *Astragalus flavus*, and *Atriplex corrugata*, 26 May 1979, S. Goodrich 12312 (Holotype BRY; isotypes distributed previously).

On 8 May 1955, I collected a peculiar *Arabis* specimen in Little Rainbow Park, Uintah County, while doing field work for my first attempt at ecological and, as it turned out, taxonomic studies. The plant was sent to a specialist in the genus for determination prior to completion of the project in 1957. It was identified initially as *A. microphylla* Nutt. ex T. & G. Subsequently, in 1976, the plant was sent again to the specialist, and this time it was determined as *A. microphylla*, with some features of *A. fernaldiana* Rollins. In May 1979, plants of a similar nature were discovered in ones Hole, east of the initial find. The plants have been compared to both *A. microphylla* and *A. fernaldiana*, of which abundant material is now at hand for comparison. The similarity to *A. microphylla* is superficial indeed, but it is very much like the material of the type variety of *A. fernaldiana*. The specimens from Rainbow Park and Jones Hole differ from the Nevada material of the type variety in having smaller flowers and from the species in having narrower siliques and shorter styles. The plants in question are separated from *A. fernaldiana* geographically by the width of Utah. They are named as follows:

***Arabis vivariensis* Welsh** sp. nov. Planta persimilis *Arabe fernaldiana* Rollins sensu lato, differt in stylis brevioribus (0.5 nec 1 mm), floribus parvioribus [prater var. *stylosam* (Wats.) Rollins], et siliquis angustioribus (1-1.5 nec 1.5-2 mm).

Plants perennial, forming mats or carpets to 1 m wide or more, the caudex branches bearing marcescent leaf bases, the branches of several seasons evident back from the branch ends, horizontally spreading to decumbent, finally erect and bearing flowering stems of the season or terminating in leafy rosettes, the flowering stems mainly 8-32 cm tall, puberulent with minute dendritic trichomes or glabrous above; basal leaves and those of the innovations 0.7-3 cm long, 1.2-4 mm wide, oblanceolate to elliptic, the blade tapering to a long, slender petiole, green to gray, pubescent overall with minute dendritic hairs, acute; cauline leaves 3-13 mm long, 1-2.5 mm wide, oblong to lanceolate or lance-subulate, puberulent to glabrous, much reduced upward; pedicels ascending to erect, 5-15 mm long in fruit, glabrous or minutely puberulent; sepals 2.5-4.5 mm long, the outer pair gibbous at the base, the inner ones less so, commonly purplish, glabrous to puberulent; petals 7-9 mm long, tapering to a basal claw, purplish; siliques 3-7 cm long, 1-1.5 mm wide, glabrous, nerved at the base, erect-ascending, typically curved or contorted, the style to 0.5 mm long; seeds uniseriate, ca 1.2 mm long, narrowly winged apically.

TYPE: USA: Utah. Uintah Co., T3S, R25E, S1, Jones Hole, National Fish Hatchery, 1,830 m, sandy calcareous gravel, Morgan Formation, 16 May 1979, S. L. Welsh & E. C. Neese 18341 (Holotype BRY; 10 isotypes to be distributed).

ADDITIONAL SPECIMENS: Utah. Uintah County, Little Rainbow Park, Dinosaur National Monument, Navajo Sandstone, sandy soil, juniper association, at 1,525 m, 8 May 1855, S. L. Welsh 152; same locality as the type, 20 June 1980, E. Neese & S. L. Welsh 8978; ibid., 24 May 1982, N. D. Atwood 8822 (all BRY).

During the spring of 1981, a new *Draba* was discovered by Ronald J. Kass, growing in crevices of granite cliffs in Goshute Canyon, Deep Creek Mountains, Tooele County, Utah. The plants appear to be shade requiring mesophytes of north-facing outcrops. An extensive field search of other canyons did not yield evidence of other specimens of the species. It is easily separated from other scapose and subscapose perennial drabas by its slenderly petiolate leaves, definite caudices clothed with persistent, filiform leaf bases, and long persistent scapes. The species does not appear to have close allies among our numerous taxa, but does share certain morphological features with *D. asprella*. The strongly branched caudex, with persistent, marcescent leaf bases and narrowly oblanceolate to spatulate leaves is diagnostic from *D. asprella*. The species is named in honor of its discoverer, as follows:

Draba kassii **Welsh** sp. nov. Planta similis *Draba asprella* generalis sed in caudicibus vestitis petiolis marcescentibus valde, foliis angustioribus et glabis supra et interdum infra, et pilis simplicibus vel furcatis differt.

Perennial, caespitose, from a definite, branching, subligneus caudex, this clothed with persistent, filiform, threadlike, leaf bases; stems 2-13 cm tall, glabrous or sparingly hirsute with mixed simple and forked to dendritic hairs; leaves all basal, rarely with 1 cauline, 1.8-4.8 cm long, 2-6 mm wide, narrowly oblanceolate to spatulate, entire or obscurely and sparingly denticulate, green, the surfaces glabrous, sparingly ciliate with simple or forked hairs; racemes simple, 2- to 9-flowered, elongating in fruit; pedicels 2-10 (15) mm long, ascending, glabrous; sepals 1.5-2.4 mm long, greenish, sparingly hairy, with simple or forked hairs; petals 4.6-5.9 mm long, yellow, obovate-spatulate, rounded; silicles 3-10 (14) mm long, 0.8-2.5 mm wide, elliptic to oblong, glabrous; styles 1-2 mm long; seeds 2-14.

TYPE: USA: Utah, Tooele Co., T10S, R18W, SW1/4 S36, Deep Creek Mtns., Goshute Canyon, granite cliff, where soil accumulates in cracks, at 2,135 m elev., on north exposure, with Juniperus osteosperma, Pinus monophylla, Lomatium grayii, etc., 8 June 1981, R. J. Kass, with Herrick 330 (Holotype BRY; 5 isotypes to be distributed).

ADDITIONAL SPECIMENS: Utah, Tooele Co., ibid, 20 May 1981, R. J. Kass 284 (BRY); ibid, 23 April 1981, R. J. Kass, with Alan Taye 243 (BRY).

The plants begin to flower while snow is still on the ground in mid-April and continue to flower to early June. They occur on granite at 2,135 to 2,500 m elevation.

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NEW SYNONYMY AND NEW SPECIES OF AMERICAN BARK BEETLES (COLEOPTERA: SCOLYTIDAE), PART XI

Stephen L. Wood[1]

ABSTRACT.—The following new generic synonymy is proposed: *Coptodryas* Hopkins (=*Microperus* Wood), *Cyrtogenius* Strohmeyer (=*Carpophloeus* Schedl, *Taphroborus* Nunberg), *Glostatus* Schedl (=*Ctonocryphus* Schedl, *Rhopalocryphus* Nunberg), *Hylurgops* LeConte (=*Hylescerites* Schedl), *Hypothenemus* Westwood (=*Ernophloeus* Nunberg), *Monarthrum* Kirsch (=*Eupteroxylon* Eggers), *Terminalinus* Hopkins (=*Kelantanius* Nunberg), *Xylechinus* Chapuis (=*Pruniphagus* Murayama), *Xylocleptes* Ferrari (=*Hylonius* Nunberg). New combinations include: *Pityophthorus anticus* Schedl is transferred to *Araptus; Hylesinus machilus* Schedl is transferred to *Phloeosinus; Phloeophthorus acaciae* Lea is transferred to *Phloeotribus; Blastophagus squamosus* Schedl is transferred to *Polygraphus; Chramesus semibrunneus* Eggers is transferred to *Pseudochramesus; Dacryophthorus capensis* Schedl is transferred to *Xylechinus; Pseudochramesus imperialis* Schedl is transferred to *Xylechinus*; and *Hoplitontus abyssinicus* Schedl is transferred to *Xylocleptes*. New specific synonymy includes: *Hypothenemus sundaensis* (Eggers) (=*Ernophloeus costalimai* Nunberg). A note on the South American *Hylesinus antipodius* Schedl is included. New names are proposed as follows: *Hylesinopsis kenyae* for *africanus* (Schedl 1963) (from *Alniphagus*) and *Hylesinopsis ugandae* for *africanus* (Schedl 1965) (from *Hylesinus*). Species described as new to science include: *Ambrosiodmus ferus* (Mexico), *Ambrosiodomus paucus* (Costa Rica), *Carphoborus bicornis* (USA), *Chaetophloeus pouteriae* (Mexico), *Cnemonyx euphorbiae* (Mexico), *Corthylus convexifrons* (Venezuela), *Corthylus senticosus* (Mexico), *Corthylus sentosus* (Mexico), *Cryptocarenus pubescens* (Brazil), *Cryptocarenus spatulatus* (Mexico), *Dendrocranulus mexicanus* (Mexico), *Hylesinus caseariae* (Mexico), *Pityophthorus levis* (USA), and *Trischidias exigua* (Mexico).

On the following pages are recorded synonymy and nomenclatural changes that affect new synonymy of 11 genera and one species and new combinations for eight species. Two new names are proposed for new junior homonyms that were created by the transfer of species from one genus to another. In addition to these changes, 14 species are described as new to science in the genera *Ambrosiodmus* (2), *Carphoborus* (1), *Chaetophloeus* (1), *Cnemonyx* (1), *Corthylus* (3), *Cryptocarenus* (2), *Dendrocranulus* (1), *Hylesinus* (1), *Pityophthorus* (1), and *Trischidias* (1). These species are from the USA (2), Mexico (9), Costa Rica (1), Venezuela (1), and Brazil (1). Under each heading the species are listed alphabetically by genus and species.

GENERIC SYNONYMY

Coptodryas Hopkins

Coptodryas Hopkins, 1915, U.S. Dept. Agric. Rept. 99:10, 54 (Type-species: *Coptodryas confusa* Hopkins, original designation)

Microperus Wood 1980, Great Basin Nat. 40:94 (Type-species: *Xyleborus theae* Eggers, original designation). *New synonymy.*

The unique female holotype of *Coptodryas confusa* Hopkins was examined and compared to more than 20 species previously placed by me in *Microperus* Wood. Notes from my previous examination of this type that were dated 1955 indicated that it was a true *Xyleborus*. However, the current revision of the tribe places it elsewhere. In my collection under the name *Xyleborus cryphaloides* Eggers, as determined by F. G. Browne, are two different species, the larger of which is identical to the type of *C. confusa*. I have not attempted to locate the type of *cryphaloides* to review its specific status, but, regardless of the outcome of such a review, the name *Microperus* Wood must be placed in synonymy as indicated above.

Cyrtogenius Strohmeyer

Cyrtogenius Strohmeyer, 1910, Ent. Blätt. 6:127 (Type-species: *Cyrtogenius bicolor* Strohmeyer, monobasic)

Carpophloeus Schedl, 1959, Tijdschr. Ent. 101:143 (Type-species: *Carpophloeus rugipennis* Schedl, monobasic). *New synonymy*

Taphroborus Nunberg, 1961, Ann. Mag. Nat. Hist. (13)3:617 (*Taphroborus vaticae* Nunberg, original designation). *New synonymy*

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Schedl named the monobasic *Carpophloeus* for *rugipennis* Schedl on the basis of the 3-segmented antennal funicle. Because the number of funicular segments is variable among the smaller species of *Cyrtogenius*, there is no way to distinguish Schedl's genus; consequently, it must be placed in synonymy as indicated above. The species *rugipennis* was based on two male and one female syntypes. Schedl (1979, Katalog der wissenschaftlichen Sammlungen des Naturhistorisches Museums in Wien 3 (Heft 2):216) designated the male in his collection as the lectotype of this species. The lectotype was examined.

Nunberg named *Taphroborus vaticae* from four specimens of undesignated sex. A "holotype" and paratype (both mounted on the same card on one pin) were deposited in the British Museum (Natural History). Because there is no way to tell which specimen is the type, both must be regarded as syntypes. The specimen that seems to fit the description most completely is a female and is still mounted on the card. The other specimen is a male and has subsequently been dislodged from the card and is missing the abdomen and ventral parts of the thorax. The female syntype is here designated as the lectotype and the male the allotype of Nunberg's species. This species falls well within the genus *Cyrtogenius*. For this reason, *Taphroborus* is placed in synonymy as indicated above.

Glostatus Schedl

Glostatus Schedl, 1939, Rev. Zool. Bot. Afr. 32:386 (Type-species: *Glostatus declividepressus*, monobasic)

Ctonocryphus Schedl, 1941, Rev. Zool. Bot. Afr. 34:398 (Type-species: *Ctonocryphus xyloctonus* Schedl, monobasic)

Rhopalocryphus Nunberg, 1967, Rev. Zool. Bot. Afr. 76:320 (Type-species: *Rhopalocryphus seydeli* Nunberg, monobasic). *New synonymy*

Following my examination of the types of most of the species of *Glostatus*, *Ctonocryphus xyloctonus* Schedl, and *Rhopalocryphus seydeli* Nunberg, I see only one moderately variable genus. The bisinuate basal margin of the pronotum and deeply impressed elytral striae of *Ctonocryphus* intergrade through *Rhopalocryphus* to *Glostatus* to such an extent that there is no possibility of making a generic division within the group. Both *Ctonocryphus* and *Rhopalocryphus* are placed in synonymy as indicated above.

Hylurgops LeConte

Hylurgops LeConte, 1876, Proc. Amer. Philos. Soc. 15:389 (Type-species: *Hylastes pinifex* Fitch =*Hylurgops rugipennis pinifex* (Fitch), subsequent designation by Hopkins 1914:123).

Hylescerites Schedl, 1947, Zentralbl. Ges. Ent. 2:29 (Type-species: *Hylescerites granulatus* Schedl, monobasic). *New synonymy*

Schedl named the monobasic fossil genus *Hylescerites* based on *H. granulatus* Schedl (1947:30) from Baltic amber. Neither the descriptions nor the photograph of the holotype indicate any characters that distinguish this genus and species from *Hylurgops*. In the absence of distinguishing generic characters, *Hylescerites* is placed in synonymy under the older name as indicated above.

Hypothenemus Westwood

Hypothenemus Westwood, 1836, Trans. Ent. Soc. London 1:34 (Type-species: *Hypothenemus eruditus* Westwood, monobasic)

Ernophloeus Nunberg, 1958, Acta Zool. Cracoviensia 2:484 (Type-species: *Ernophloeus costalimai* Nunberg =*Stephanoderes sundaensis* Eggers, original designation). *New synonymy*

The female holotype and two female paratypes of *Ernophloeus costalimae* Nunberg were examined and compared directly to my female homotypes of *Stephanoderes sundaensis* Eggers. Because they are quite clearly congeneric with *Hypothenemus eruditus* Westwood, Nunberg's genus must be placed in synonymy under *Hypothenemus* and his species under *sundaensis* as indicated above.

Monarthrum Kirsch

Monarthrum Kirsch, 1866, Berliner Ent. Zeitschr. 10:213 (Type-species: *Monarthrum chapuisii* Kirsch, monobasic)

Eupteroxylon Eggers, 1936, Rev. de Ent. 6:392 (Type-species: *Eupteroxylon comatum* Eggers, monobasic)

The female holotype of *Eupteroxylon comatum* Eggers is in the *laterale* Eichhoff species group of *Monarthrum*. The holotype of *comatum* was compared to a series of females of (*Cosmocorynus*) *latus* Schedl from Colombia. The Eggers species is smaller but has almost identical antennae, and they share the same general sculptural design of frons and elytra. They are obviously congeneric. For this reason, *Eupteroxylon* is placed in synonymy as indicated above.

Terminalinus Hopkins

Terminalinus Hopkins, 1915, U.S. Dept. Agric. Rept. 99:10, 57 (Type-species: *Terminalinus terminaliae* Hopkins, original designation)

Kelantanius Nunberg, 1961, Ann. Mag. Nat. Hist. (13)3:621 (Type-species: *Xyleborus punctatopilosus* Schedl, original designation). *New synonymy*

The unique female holotype of *Terminalinus terminaliae* Hopkins was examined and compared to material in my collection. It is in the same species group with *Xyleborus major* Stebbing, *X. latus* Eggers, *X. siclus* Schedl, *X. pseudopilifer* Schedl, *X. postecipilosus* Schedl, *pilifer* Eggers, *pseudomajor* Schedl, *xanthophyllus* Schedl, and *macropterus* Schedl. Because this species group makes up part of the genus previously known as *Kelantanius* Nunberg, Nunberg's name must be placed in synonymy under the older name *Terminalinus* as indicated above.

Xylechinus Chapuis

Xylechinus Chapuis, 1869, Synopsis des Scolytides, p. 36 (Type-species: *Hylesinus (Dendroctonus) pilosus* Ratzeburg, monobasic)

Pruniphagus Murayama, 1958, Bull. Fac. Agric. Yamaguti Univ. 9:930 (Type-species: *Pruniphagus gummensis* Murayama, original designation)

The "holotype" and "allotype" of *Pruniphagus gummensis* Murayama are mounted on the same pin. Because the description is composite, both specimens are female, and there is no clue in the description as to which is the type, I here designate the upper female that has one unbroken antenna (the club is lost on the other side of the type and on both sides in the lower specimen) as the lectotype of this species. This species is very closely allied to *Xylechinus padi* Wood but it is distinct. These two species are members of *Xylechinus*, although the scales on the pronotum and elytra are rather small and slender and the setae on the metepisternum are palmately divided. This placement requires that *Pruniphagus* be placed in synonymy as indicated above.

Xylocleptes Ferrari

Xylocleptes Ferrari, 1867, Die Forst- and Baumsucht-schädlichen Borkenkäfer, p. 37 (Type-species: *Bostrichus bispinus* Duftschmidt)

Hylonius Nunberg, 1973, Exploration du Parc Nacional des Virunga (2)23:16 (Type-species: *Hylonius brunneus* Nunberg, original designation). *New synonymy*

A paratype of *Hylonius brunneus* Nunberg was examined. It is congeneric with *Xylocleptes bispinus* (Duftschmidt); consequently, *Hylonius* must be placed in synonymy as indicated. The status of Nunberg's species was not investigated.

NEW COMBINATIONS

Araptus anticus (Schedl), n. comb.

Pityophthorus anticus Schedl, 1976, Ent. Abh. Mus. Tierk. Dresden 41:66 (Holotype, female; Río Negro, Brasil; Wien Nat. Mus.)

In the original treatment of *Pityophthorus anticus* Schedl, the sexes were reversed. This species is a member of the genus *Araptus* and is here transferred to that genus.

Phloeosinus machilus (Schedl), n. comb.

Hylesinus machilus Schedl, 1959, Indian For. Rec., n.s., Ent. 9(8):173 (Paratype; Chachpur, Chakrata, Uttar Pradesh, India; Wien Nat. Mus.; holotype lost, if it ever existed)

None of the type specimens, including the holotype of this species, that were sent by the Forest Research Institute to Schedl for study were ever returned to the FRI. After examining the loan sheets at FRI, the nontype material returned by Schedl, and the FRI specimens retained by Schedl from that loaned material, I suspect that the holotypes cited by Schedl in the descriptions of FRI species never existed. A consequence of that action is seen in the description of *Hylesinus machilus* Schedl. The head and prothorax of Schedl's paratype of this species are missing. As a result, Schedl named this species in the wrong genus even though it had been sent to him under the clearly marked manuscript designation of *Phloeosinus machili* Beeson (nomen nudum).

I have examined more than 50 specimens of this species from Uttar Pradesh, several of which bear data identical to that published by Schedl. As indicated above, it must be transferred to *Phloeosinus*.

Phloeotribus acaciae (Lea), n. comb.

Phloeophthorus acaciae Lea, 1910, Proc. Roy. Soc. Victoria, n.s., 22:146 (Syntypes; Tasmania)

A series of this species was found in the Schedl Collection (Wien Nat. Mus.). Because the genus is unknown in the area from southern Asia to Australia, except for this species, it is of special interest. The three terminal segments of the antenna are no wider than those of the funicle, smaller than in *rhododactylus* (Marsham) of Europe. This and other primitive characters suggest that this species was derived from South American stock prior to the Tertiary and has been preserved with little modification. The scutellum is not visible. Schedl (1938, Proc. Linn. Soc. N.S.W. 83:216) erroneously placed the species in *Xylechinus*, a genus quite unrelated to the one to which it belongs.

Polygraphus squamosus (Schedl), n. comb.

Blastophagus squamosus Schedl, 1975, Ent. Basil. 1:384 (Holotype; Bhutan, Dorjula; Nat. Mus. Basel)

The species named *Blastophagus squamosus* Schedl is represented in the Schedl material at Wien by one paratype. This specimen fits the description of the species, but it is a member of *Polygraphus* and must be transferred to that genus.

Pseudochramesus semibrunneus (Eggers), n. comb.

Chramesus semibrunneus Eggers, 1950, Ent. Blätt. 45–46:145 (Holotype, male; Brasil; Wien Nat. Mus.)

Schedl had the sexes reversed in this genus. The male holotype of *Chramesus semibrunneus* Eggers was examined. It is a member of the genus *Pseudochramesus* and is here transferred to the genus as indicated above.

Xylechinus capensis (Schedl), n. comb.

Dacryophthorus capensis Schedl, 1971, Opusc. Zool. Munchen 119:6 (Holotype, female; Cape Prov., South Africa; Wien Nat. Mus.)

The female holotype of *Dacryophthorus capensis* Schedl belongs to the genus *Xylechinus* and is here transferred to that genus.

Xylechinus imperialis (Schedl), n. comb.

Pseudochramesus imperialis Schedl, 1958, Acta Zool. Lilloana 16:39 (Lectotype, male; Wien Nat. Mus., present designation)

The original description of *Pseudochramesus imperialis* Schedl is composite. The "holotype" cited by Schedl (1979:122) and so labeled in his collection is here designated as the lectotype of this species. An abundance of characters indicates that it belongs to the genus *Xylechinus*. A second male in the Schedl Collection is labeled as the "holotype" of *Xylechinus calvus* Schedl. Because I have found no description associated with this name, it is presumed to be a nomen nudum.

Xylocleptes abyssinicus (Schedl), n. comb.

Hoplitontus abyssinicus Schedl, 1965, Rev. Ent. Moçambique 8:364 (Holotype; Abyssinien; Wien Nat. Mus.)

The holotype of *Hoplitontus abyssinicus* Schedl is almost totally covered by glue. It definitely is a member of the Dryocoetini and probably is in *Xylocleptes*. A more precise identification must await a time when the glue can be dissolved to expose additional characters.

NEW NAMES

Hylesinopsis kenyae, n. n.

Alniphagus africanus Schedl, 1963, Ent. Abh. Ber. Mus. Tierk. Dresden 28:259 (Holotype; Riff Valley, Kenya; Wien Nat. Mus.) *Preoccupied*

The species named *Alniphagus africanus* Schedl is a member of the genus *Hylesinopsis*. Because the transfer of this species causes it to become a junior homonym of *africanus* (Eggers 1933), a replacement name is needed. The new name *kenyae* is proposed as a replacement for the Schedl species.

Hylesinopsis ugandae, n. n.

Hylesinus africanus Schedl, 1965, Nova Taxa Ent. 38:4 (Holotype; Mpanga, Uganda; British Mus. Nat. Hist.). *Preoccupied*

The transfer of *Hylesinus africanus* Schedl to *Hylesinopsis* makes this species a junior secondary homonym of *africanus* (Eggers 1933). The new name *ugandae* is proposed as a replacement for the Schedl species.

SPECIAL NOTE

Hylesinus antipodius Schedl

Hylesinus antipodius Schedl, 1951, Rev. Chil. Ent. 1:17 (Syntypes; Rengo, Chile; Wien Nat. Mus. and Museo Nacional de Historia Natural, Santiago)

Hylesinus antipodius Schedl is the only known true member of this genus in America south of Guatemala. The elytral scales are more slender than in any North American species. It appears to be more closely allied to *H. cordipennis* Lea, from Australia, than to any other species known to me. If this is correct, then *H. antipodius* would probably have been derived from Australian stock prior to the Tertiary when island hopping was still possible between these separating land masses.

NEW TAXA

Ambrosiodmus ferus, n. sp.

This species is clearly allied to *divexulus* Wood, although only one suture is on the posterior face of the antennal club. It is distinguished from *divexulus* by the larger size, by the more gradual, more finely punctured elytral declivity, and by other characters described below.

FEMALE.—Length 2.6 mm (paratypes 2.5–2.7 mm), 2.4 times as long as wide; color black.

Frons about as in *divexulus* except a weak median carina present on upper half.

Pronotum as in *divexulus* except summit more distinct, asperities behind summit slightly larger and closer.

Elytra similar to *divexulus* except discal strial punctures slightly larger, not as deep, interstrial punctures smaller, not as deep; declivity more gradual, particularly on upper half, interstriae 1 not elevated; vestiture finer, slightly larger.

TYPE LOCALITY.—Jalapa, Veracruz, Mexico.

TYPE MATERIAL.—The female holotype and five female paratypes were taken at the type locality on 16-VIII-1983, FANM-33, from *Quercus*, by Felipe A. Noguera.

The holotype and paratypes are in my collection.

Ambrosiodmus paucus, n. sp.

This species is distinguished from *divexulus* Wood by characters described below.

FEMALE.—Length 1.9 mm (paratypes 1.8–1.9 mm), 2.2 times as long as wide; color very dark brown.

Frons about as in *divexulus* except central three-fourths without reticulation, shining.

Pronotum similar to *divexulus* except reticulation absent, asperities on posterior half distinctly larger, closer.

Elytra similar to *divexulus* except discal punctures of medium size, confused, striae not indicated; declivity as in *divexulus* except strial and interstrial punctures distinctly smaller, interstriae 1 armed as on 3; declivital vestitute stouter, of more uniform length.

TYPE LOCALITY.—Isla del Coco, Costa Rica.

TYPE MATERIAL.—The female holotype and three female paratypes were taken at the type locality in April 1980 by George Stevens.

The holotype and paratypes are in my collection.

Carphoborus bicornis, n. sp.

This species is distinguished from *bifurcus* Eichhoff by the frontal and declivital characters that are described below.

FEMALE.—Length 1.5 mm (paratypes 1.3–1.6 mm), 2.5 times as long as wide; color dark brown, vestiture pale.

Frons convex, flattened on lower two-thirds on median half, surface reticulate; a pair of rather widely spaced, conspicuous hornlike spines just below upper level of eyes on median two-thirds, each two or more times as high as basal width in Alabama series, about as high as wide and blunt in Florida series, ventral surface of each spine with a few scales.

Pronotum and elytra as in *bifurcus* except declivital interstriae 3 with crest of elevation wider, denticles more numerous and much more strongly confused.

MALE.—Similar to female except frons as in male *bifurcus*.

TYPE LOCALITY.—Fayette, Alabama.

TYPE MATERIAL.—The female holotype, male allotype, and two paratypes were taken at the type locality V-159-10037, from *Pinus*, by Walter Grimes. Fourteen paratypes were taken at Archibold Biological Station, Lake Placid, Florida, 7 March 1984, *Pinus clausa*, by Mark Deyrup.

The holotype, allotype, and paratypes are in my collection.

Chaetophloeus pouteriae, n. sp.

This species is distinguished from *insularis* (Blackman) as indicated by characters described below. This is the third species in the group lacking submarginal crenulations behind the marginal row at the base of the elytra.

MALE.—Length 1.2 mm (paratypes 1.1–1.2 mm), 1.8 times as long as wide; color dark brown, vestiture pale.

Frons as in *insularis* except impression less extensive above eyes.

Pronotum as in *insularis* except punctures much smaller, more definite, spaces between punctures almost smooth; scales shorter, broader, those on anterior margin conspicuously longer.

Elytra as in *insularis* except strial punctures deeper, very slightly larger; scales in ground cover much stouter.

FEMALE.—Similar to male except frons almost flat on lower half, convex above.

TYPE LOCALITY.—Campo Experimental. INIF, Escarcega, Campeche, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and six paratypes were taken at the type locality on 9-I-1984, AEV-85, *Pouteria campechana*, by A. Estrada V.

The holotype, allotype, and paratypes are in my collection.

Cnemonyx euphorbiae, n. sp.

This species is distinguished from *splendens* Wood by characters described below.

FEMALE.—Length 2.5 mm (male paratypes 2.3 mm), 2.04 times as long as wide; color reddish brown.

Frons with median two-thirds from epistoma to upper level of eyes rather abruptly, concavely impressed, impressed area densely, rather coarsely punctured and ornamented by numerous, erect, rather stout setae of uniform length; epistoma not subcarinate as in *splendens*. Antenna about as in *splendens*.

Pronotum as in *splendens* except anterior constriction more distinct, punctures coarser and closer.

Elytra about as in *splendens* except interstrial punctures confused, declivital interstriae less strongly elevated, declivital interstrial setae much smaller, almost obsolete, hairlike.

MALE.—Similar to female except frons convex, glabrous, punctures less dense.

TYPE LOCALITY.—Cañon de Lobos, Yautepec, Morelos, Mexico.

TYPE MATERIAL.—The female holotype, male allotype, and two male paratypes were taken at the type locality on 14 Marzo 1984, 1,400 m, SM-247, by Edgar Martinez F.

The holotype, allotype, and paratypes are in my collection.

Corthylus convexifrons, n. sp.

This species is unique and does not fit into any known species group. The female frons is convex and glabrous, the general pronotal and elytral features are much as in the larger *Corthylocurus* species.

FEMALE.—Length 3.4 mm (paratypes 2.9–3.6 mm), 2.4 times as long as wide; rather light reddish brown.

Frons evenly, strongly convex, median fourth with a slight elevation, a small median tubercle on elevation; surface finely reticulate, punctures minute, sparse; glabrous. Antennal club slightly asymmetrical, two feebly procurved sutures present; posterior face bearing a small tuft of hair arising from lateral half of all three segments, extending slightly beyond tip of club.

Pronotum 1.1 times as long as wide; sides almost straight and subparallel on basal half, broadly rounded in front; anterior margin subcostate, with about eight weak serrations indicated; posterior half reticulate, punctures sparse, minute. Glabrous.

Elytra 1.36 times as long as wide, 1.44 times as long as pronotum; sides almost straight and parallel on basal three-fourths, very broadly rounded behind; disc subreticulate, punctures small, shallow, distinct, confused. Declivity very steep, shallowly sulcate on median third; lateral margins on upper half armed by two pairs of small, blunt tubercles; a weak ventrolateral margin indicated on median third. Almost glabrous.

MALE.—Similar to female except epistomal elevation poorly formed, anterior margin of pronotum with two coarse serrations, declivital impression slightly stronger.

TYPE LOCALITY.—La Mucuy, 20 km west of Merida, Merida, Venezuela.

TYPE MATERIAL.—The female holotype, male allotype, and 13 paratypes were taken at the type locality on 12-XI-1969, 2,500 m, No. 131, from an unidentified tree branch, by me. Paratypes include: 6 from the type locality taken 22-XII-1969, No. 207, from a tree seedling; 19 from La Carbonera Experimental Forest, 50 km west of Merida, Merida Venezuela, 9-XII-1969, 2,500 m, No. 174 from *Nectandra* branches; all were taken by me.

The holotype, allotype, and paratypes are in my collection.

Corthylus senticosus, n. sp.

This species is distinguished from *sentus* Wood by characters of the frons, antenna, and elytral declivity as described below.

FEMALE.—Length 1.5 mm (allotype 1.8 mm), 2.1 times as long as wide; color very dark brown.

Frons extensively excavated as in *sentus* except vestiture on vertex slightly shorter, lateral spongy areas slightly larger, a large longitudinal, cylindrical, subcarinate elevation extending from just above epistoma to just below middle of frons; excavated area glabrous except for fringe of long hair on vertex. Antennal club much less asymmetrical.

Pronotum as in *sentus*.

Elytra resembling *sentus* except disc mostly subreticulate, punctures mostly obsolete; declivity steeper, interstriae 2 on upper third rather strongly, narrowly elevated and armed by small, pointed denticles to middle of declivity, sutural interstriae not elevated or armed.

MALE.—Similar to female except frons convex, reticulate, subglabrous; anterior margin or pronotum armed by two serrations.

TYPE LOCALITY.—Jalapa, Veracruz, Mexico.

TYPE MATERIAL.—The female holotype and male allotype were taken at the type locality on 23-X-1983, FANM-77, from *Psitacanthus schiedeanus*, by Felipe A. Noguera.

The holotype and allotype are in my collection.

Corthylus sentosus, n. sp.

This species is distinguished from *sentus* Wood by characters of the frons, antenna, and elytral declivity as described below.

FEMALE.—Length 1.9 mm (allotype and paratype 2.0 mm), 2.3 times as long as wide; color very dark brown.

Frons as in *sentus* except spongy areas more widely separated below but extending well above upper level of eyes laterally, their inner margins on upper half each bearing a row of about six long, coarse setae, setae on vertex much shorter. Antennal club about as in *senticosus* Wood.

Pronotum as in *sentus* except disc without crenulations.

Elytra as in *sentus* except devoid of punctures, uniformly subreticulate; declivity reticulate, interstriae 2 on middle half distinctly, rather weakly elevated, crest of this elevation armed by a row of four fine denticles.

MALE.—Similar to female except frons convex, reticulate, subglabrous; anterior margin of pronotum armed by two small serrations.

TYPE LOCALITY.—Km 32 on Carretera Patzcuaro-Ario de Rosales, Michoacán, Mexico.

TYPE MATERIAL.—The female holotype, male allotype, and one female paratype were taken on 31-X-1980, 2,360 m, S-130, from *Psiticanthus* sp., by T. H., Atkinson and Armando Equihua.

The holotype, allotype, and paratype are in my collection.

Cryptocarenus pubescens, n. sp.

This unique species is the largest, stoutest, most pubescent member of the genus.

FEMALE.—Length 3.1 mm, 2.3 times as long as wide; color reddish brown.

Frons broadly convex; coarsely, closely, subrugosely punctured from epistoma to vertex; median line from upper level of eyes with an impunctate, transversely strigose, low, subcarinate elevation; vestiture fine, rather long, moderately abundant. Antennal sutures more strongly procurved than usual for this genus.

Pronotum as long as wide; sides weakly arcuate and subparallel on basal half, somewhat narrowly rounded in front, anterior margin armed by 14 serrations; anterior slope armed by numerous asperities of moderate size; posterior areas finely punctured, punctures on disc finely granulate. Vestiture of fine, erect, rather abundant hair.

Elytra 1.4 times as long as wide, 1.4 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; surface almost smooth and shining, punctures rather small, shallow, confused, rather close. Declivity rather steep, convex; surface obscurely reticulate, punctures as on disc.

TYPE LOCALITY.—Sixty-nine km north of Manaus, Brazil.

TYPE MATERIAL.—The unique female holotype was taken at the type locality on 7-XII-1979, by George Stevens.

The holotype is in my collection.

Cryptocarenus spatulatus, n. sp.

This species is distinguished from *lepidus* Wood by characters described below.

FEMALE.—Length 1.8 mm (Paratypes 1.8 mm), 2.5 times as long as wide; color dark reddish brown.

Frons as in *lepidus* except subparallel aciculations on upper two-thirds of frons deeper.

Pronotum about as in *lepidus* except asperities much coarser, resembling *Hypothenemus*; anterior margin armed by 6–8 serrations.

Elytra as in *lepidus* except declivity steeper; strial punctures more deeply impressed, interstriae more regularly punctured; vestiture extending to base on at least odd-numbered interstriae, regular on posterior half of elytra on all interstriae, much more closely spaced than in *lepidus*, each seta erect, strongly flattened on its distal half, about twice as wide as in *lepidus*.

TYPE LOCALITY.—Sta. María Chimalpa, Oaxaca, Mexico.

TYPE MATERIAL.—The female holotype and seven paratypes were taken at the type locality on 10-II-1984, 250 m, S-977, *Struthanthus*, by Armando Equihua. One paratype is labeled 5 mi N. Mazatlan, Sinaloa, Mexico, 24-VII-1964, H. F. Howden. A specimen, not designated as a paratype, is labeled Peru, 12-IX-1963, E. M. Jones, in derus plant intercepted at Miami.

The holotype and seven paratypes are in my collection; one paratype is in the Canadian National Collection.

Dendrocranulus mexicanus, n. sp.

This species is distinguished from the allied *costaricensis* Eggers by the characters described below.

FEMALE.—Length 2.5 mm (paratypes 2.2–2.5 mm), 2.7 times as long as wide; color very dark brown.

Frons as in *costaricensis* except punctures mostly finely granulate; vestiture equal in abundance but conspicuously shorter and of darker color.

Pronotum as in *costaricensis* except punctured area smaller, asperities slightly larger and more extensive in posterolateral areas; punctures in discal area mostly with fine granule on lateral margin.

Elytra as in *costaricensis* except surface on basal fourth of disc more wrinkled; declivity not quite as steep, strial punctures smaller, fine interstrial granules replace punctures; vestiture similar but finer on disc and declivity.

MALE.—Similar to female except frons more strongly convex above, punctures obscure except laterally, vestiture sparse, inconspicuous; elytral declivity similar to *costaricensis* except not as steep, more strongly impressed on interstriae 2, 3 higher, granules on 2 not evident; setae a bit more slender.

TYPE LOCALITY.—Naolinco, Veracruz, Mexico.

TYPE MATERIAL.—The female holotype, male allotype, and six paratypes were taken at the type locality on 28-I-1984, FANM-120, from *Sechium edulis*, F. A. Noguera M.

The holotype, allotype, and paratypes are in my collection.

Hylesinus caseariae, n. sp.

This species is distinguished from *californicus* Swaine by the more deeply, more broadly impressed male frons, by the less distinct, slightly longer female frontal carina, by the less strongly impressed declivital interstriae 2 in both sexes, and by the smaller, stouter scales on pronotum and elytra.

MALE.—Length 2.5 mm (paratypes: male 2.8 mm, females 2.6 mm), 1.8 times as long as wide; color pattern as in *californicus* except with more dark brown scales, fewer pale scales.

Frons resembling *californicus* except impression deeper, extending higher on vertex, much broader, lateral margins higher, more abruptly rounded to upper level of eyes; median line feebly elevated.

Pronotum about as in *californicus* except rugose-reticulation stronger, asperities apparently smaller and more numerous, scales smaller, usually stouter.

Elytra similar to *californicus* except interstriae 2 very slightly less strongly impressed, tubercles on 1 and 3 and base of 2 smaller, closer, more definite; erect scales on 1 more slender, each 2.5–3.0 times as long as wide, those on 3–7 distinctly smaller, slender setae on 8, 9, and basal half of 7 much more slender, hairlike; scales in ground cover smaller, stouter.

FEMALE.—Similar to male except frons basically convex as in *californicus* except carina lower and slightly longer; declivital interstriae 3 not impressed, resembling 1 and 3, erect scales normal, not enlarged.

TYPE LOCALITY.—Acajete, Veracruz, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and one male and one female paratype were taken at the type locality on 22-XI–1983, FANM-92, from *Casearia* (Flacourtiaceae), by Felipe A. Noguera.

The holotype, allotype, and paratypes are in my collection.

Pityophthorus levis, n. sp.

This species is distinguished from the *boycei* Swaine and the *comosus* Blackman groups of species by the virtually impunctate, subglabrous frons that is not sexually dimorphic and by the elytral declivity that resembles neither group.

FEMALE.—Length 2.5 mm (paratypes 2.2–2.7 mm), 2.7 times as long as wide; color dark brown, elytra often reddish brown.

Frons broadly convex; surface smooth, shining, a few minute punctures; subglabrous, a few fine, short setae usually present. Antennal club resembling *comosus* except sutures almost straight.

Pronotum resembling *comosus* except summit not as high, punctures on posterior areas considerably smaller, shallow, much more widely spaced.

Elytra resembling *boycei* except discal punctures slightly larger and less numerous, confused, declivity steeper, lateral convexities more abrupt, interstriae 2 narrower on lower half, tubercles (about 6) conspicuously larger. Vestiture fine, rather long on declivity, absent on interstriae 2, very short on 1.

TYPE LOCALITY.—Fifteen miles northwest of Flagstaff, Arizona (Hart's Prairie Road).

TYPE MATERIAL.—The female holotype, male allotype, and 13 paratypes were taken at the type locality on 18-IX-1984, from lateral shoots of *Pinus ponderosa*, by M. R. Wagner.

Trischidias exigua, n. sp.

This is the fourth species named in this genus. It is distinguished from the closely allied *atoma* (Hopkins) as described below.

FEMALE.—Length 0.8 mm (paratypes 0.8–0.9 mm), 2.1 times as long as wide; color very dark brown, almost black.

Frons as *atoma* except without a median impression.

Pronotum resembling *atoma* except anterior margin armed by four serrations, asperities higher and apparently less numerous, surface smooth, shining, without any indication of reticulation. Vestiture mostly hairlike, a few stouter setae on posterior areas.

Elytra about as in *atoma* except strial punctures much smaller, weakly impressed, interstrial granules much smaller (half as large), erect interstrial scales of equal length but only half as wide, each about four times as long as wide.

TYPE LOCALITY.—Campo Experimental, INIF, Escarcega, Campeche, Mexico.

TYPE MATERIAL.—The female holotype and six paratypes were taken at the type locality on 15-II-1984, AEY-111 from *Belotia campbelli*, by A. Estrada V.

After the above description was prepared, a series from southern Florida was examined. These are not part of the type series.

The holotype and paratypes are in my collection.

ENERGY AND PROTEIN CONTENT OF COYOTE PREY IN SOUTHEASTERN IDAHO

James G. MacCracken[1,2] and Richard M. Hansen[1]

ABSTRACT.—Gross energy, digestible energy, crude protein, and digestible crude protein were estimated for two leporids and five rodents that were the primary prey of coyotes (*Canis latrans*) in southeastern Idaho. Digestible protein estimates differed (38%–54%) more than digestible energy (3.5–4.4 kcal), in the prey examined.

Information on the energy and nutrient content of small mammals that are the food of coyotes (*Canis latrans*) is necessary to evaluate prey selection (Pyke et al. 1977). In addition, those data are valuable in ecological studies of other predators, and for research on nutrient cycling and energy flow through ecosystems (Golley 1960, Odum et al. 1962, Weigert 1965, Fleharty et al. 1973). Research has shown that energy composition of some small mammal bodies varies seasonally and geographically (Gorecki 1965, Fleharty et al. 1973, Cameron et al. 1979), which indicates that the use of data from the immediate study area may be necessary.

The purpose of this study was to estimate the gross and digestible energy and crude protein and digestible crude protein of small mammals in conjunction with a study of coyote feeding strategies (Johnson and Hanson 1979, MacCracken and Hansen 1982). Large differences in prey body composition might influence coyote food selection.

METHODS

Small mammals were collected from the Idaho National Engineering Laboratory (INEL) Site in southeastern Idaho (≃113°00′W, 44°00′N). The INEL Site occupies about 231,500 ha of the Upper Snake River Plain. The dominant vegetation of the study area was a sagebrush/bunchgrass (*Artemisia/Agropyron*) shrubsteppe. Dr. B. L. Keller of Idaho State University supplied five specimens each of the deer mouse (*Peromyscus maniculatus*), Townsend's ground squirrel (*Spermophilus townsendii*), Ord's kangaroo rat (*Dipodomys ordii*), and least chipmunk (*Eutamias minimus*). All specimens were trapped during the summer of 1982 and frozen. Additionally, five specimens each of the black-tailed jackrabbit (*Lepus californicus*), Nuttall cottontails (*Sylvilagus nuttallii*), and montane vole (*Microtus montanus*) were collected during July 1983 and frozen.

Frozen specimens were chopped into approximately 1 cm^3 pieces, oven-dried at 60 C for 72 h, then ground in a Willey Mill to pass through a 2-mm mesh screen. Samples were then submitted to the Nutrient Analysis Lab, Colorado State University, to determine gross energy (kcal/g dry matter) by bomb calorimetry and crude protein (% dry matter) by Kjeldahl nitrogen (× 6.25), in duplicate for each individual animal.

The digestible fraction of each species was estimated using the data of Johnson (1978). Litvaitis and Mautz (1980) reported similar results from feeding trials with captive coyotes. Using Johnson's estimates, digestible energy and protein were calculated for each species on a dry weight basis.

Analysis of variance, followed by Tukey's mean separation procedure, was used to test for differences in mean gross energy and crude protein among the species examined ($P = 0.05$). Adequacy of sample size ($N = 5$) for each species for gross energy and crude protein estimates was assessed using a standard formula based on the *t* distribution (Giles 1971:158). Adequate sample size (N_e) precision levels were set so as to permit estimates within 10% of the mean with 95% confidence.

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Table 1. Mean (SE) gross energy (kcal/g dry matter), digestible gross energy[1], crude protein (% dry matter), and digestible crude protein of coyote prey on the Idaho National Engineering Laboratory in southeastern Idaho. N_e is estimated adequate sample size[2] for gross energy and crude protein values.

	Energy			Protein		
Species	Gross	N_e	Digestible	Crude	N_e	Digestible
Lepus californicus	4.8(0.1)	2	3.8(0.2)	64.0(1.3)	2	50.6(1.3)
Sylvilagus nuttallii	5.0(0.2)	4	4.1(0.2)	65.4(2.5)	5	53.6(2.5)
Microtus montanus	5.0(0.2)	4	3.9(0.2)	65.4(2.5)	5	51.0(2.5)
Peromyscus maniculatus	5.1(0.1)	1	3.9(0.2)	62.5(1.9)	3	47.5(1.9)
Spermophilus townsendii	5.6(0.4)	19	4.4(0.4)	48.5(4.1)	26	38.3(4.1)
Dipodomys ordii	4.6(0.1)	2	3.5(0.1)	62.7(1.4)	2	47.7(1.4)
Eutamias minimus	4.9(0.1)	2	3.9(0.1)	60.4(1.9)	4	48.3(1.9)

[1] Estimates of the digestible fraction (% dry matter) of each species were reported by Johnson (1978).

[2] Adequate sample size was determined using a standard formula based on the *t* distribution (Giles 1971: 158).

Results and Discussion

Mean gross energy estimates ranged from 4.6 to 5.6 kcal/g and were greatest ($P < 0.03$) for the Townsend's ground squirrel (Table 1). The other small mammals examined were similar in energy content except Ord's Kangaroo rat, which was the lowest ($P < 0.03$).

Mean digestible gross energy ranged from 3.5 to 4.1 kcal/g being greatest ($P > 0.05$) for the Townsend's ground squirrel, and lowest ($P > 0.05$) for Ord's kangaroo rat (Table 1).

Mean crude protein estimates ranged from 48.5 to 65.4% (Table 1). Crude protein was lowest ($P < 0.04$) in Townsend's ground squirrel and greatest ($P > 0.05$) for the Nuttall cottontail and montane vole. Digestible protein ranged from 38.3% for Townsend's ground squirrel to 53.6% for Nuttall cottontail.

Five individuals of each species were adequate to estimate energy and protein content, except for Townsend's ground squirrel (Table 1). The large variation in energy and protein content for Townsend's ground squirrel appeared to be related to fat content because some individuals had considerable fat, whereas other did not. This was probably attributable to specimens originating from different cohorts and/or captured at different stages in the annual fat cycle.

Our gross energy estimates were similar to those of other published studies which examined the same species or genera. Gorecki (1965) reported a mean (± SD) summer estimate of 5.1 (± 0.5) kcal/g for *Microtus arvalis*, which is 0.1 kcal/g greater than our estimate for montane voles. Fleharty et al. (1973) examined energy content of four rodents, including the deer mouse and prairie vole (M. *ochrogaster*). They reported seasonal extremes ranging from 5.05 to 5.14 kcal/g for the deer mouse and 4.91 to 5.01 kcal/g for the prairie vole. The maximum values of Fleharty et al. (1973) are similar to our data for the deer mouse and montane vole. Gorecki (1965) stated that energy values were greatest in summer in his study. Davison et al. (1978) examined energy content of the snowshoe hare (*Lepus americanus*), meadow vole (M. *pennsylvanicus*), and white-footed mouse (P. *leucopus*) collected from October through January. Their data are similar to ours for species of the same genus. Litvaitis and Mautz (1980) presented energy estimates for the snowshoe hare (4.97 kcal/g) and laboratory mouse (*Mus musculus*) (6.00 kcal/g), but collection dates were not given. Both of those estimates are higher than we observed for the black-tailed jackrabbits and deer mouse.

Few studies have examined crude protein levels of wild mammals (Davison et al. 1978, Litvaitis and Mautz 1980). Energy is typically the currency used in modeling foraging theory and in experiments testing those models (Pyke et al. 1977). However, Davies (1977) suggested that nutrients as well as energy may be important in prey selection, and Pulliam (1974) cited protein as having potential importance. Mean crude protein levels for the black-tailed jackrabbit estimated in our study were 6% to 8% lower than those reported for the snowshoe hare by Davison et al. (1978) and Litvaitis and Mautz (1980). Protein levels for the deer mouse reported here were 3% to 9% greater than those reported for the white-footed mouse (Davison et al. 1978) and laboratory mouse (Litvaitis and Mautz 1980).

Our results and those of Davison et al. (1978) and Litvaitis and Mautz (1980) indicate that percent crude protein varies among species more than does gross energy. This observation suggests that generalizations about protein content of animal bodies across species lines are of limited value. However, our conclusions and those of other studies cited herein suggest that gross energy levels are similar among species and locales.

To what degree coyotes are able to detect differences in prey body composition is unknown. Digestible energy ranged from 3.5 to 4.4 kcal/g dry matter, or a 25% difference. Apparently, prey abundance, body size, and/or defensive strategies may be more important in coyote prey selection. However, digestible protein estimates ranged from 38% to 54%, or a 42% difference. Protein could be important in prey selection. Furthermore, other nutrients and trace elements should be studied.

ACKNOWLEDGMENTS

We thank O. D. Markham, W. J. Arthur, and D. K. Halford for their assistance in this study. R. J. Gates and M. P. Stafford helped collect leporids. B L. Oskroba analyzed the specimens. Dr. B. L. Keller is thanked for the use of rodents captured during his studies on the INEL site. The Agricultural Experiment Station, University of Alaska, Palmer, Alaska, kindly provided facilities for the completion of this research. This study was funded by the U.S. Department of Energy, Idaho Operations Office, INEL Ecology Program.

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ESTIMATES OF SITE POTENTIAL FOR DOUGLAS-FIR BASED ON SITE INDEX FOR SEVERAL SOUTHWESTERN HABITAT TYPES

Robert L. Mathiasen[1], Elizabeth A. Blake[1], and Carleton B. Edminster[2]

ABSTRACT.—Estimates of site potential for Douglas-fir based on measured site indexes in 450 stands are compared between 10 southwestern habitat types. Significant differences in site potential are found between the habitat types studied.

Site index is currently the most widely used method of evaluating site quality or potential productivity of forest lands in the United States (Jones 1969, Husch et al. 1972, Daubenmire 1976). Site index is based on the average heights of dominant and codominant trees at a specified index age (usually 50 or 100 years). Because stands of the index age are seldom encountered, site index curves are constructed to allow for estimation of site index for stands older or younger than the index age by interpolation between the curves. Site index curves describe the height growth of hypothetical trees of specified site indexes.

The use of habitat types (Daubenmire 1952) to classify forest vegetation is gaining acceptance by land managers and researchers in the western United States (Layser 1974, Pfister 1976, Pfister and Arno 1980). One of the primary uses of habitat types is in timber management. Habitat types are used to compare regeneration success, succession patterns, cutting methods, and timber productivity and to develop guidelines for collecting seed and planting nursery stock (Pfister and Arno 1980).

The use of habitat types to predict forest site productivity potential is proposed by several investigators. Differences in the rate of height growth by habitat type are demonstrated for several tree species (Daubenmire 1961, Deitschman and Greene 1965, Stanek 1966, Stage 1975, Hoffman 1976). Significant differences between site indexes are also shown for habitat types (Stanek 1966, Stage 1975, Hoffman 1976). Pfister et al. (1971, 1977) and Steele et al. (1981) use site index curves and normal yield tables to estimate yield capability for habitat types in Montana and Idaho.

Southwestern forests are becoming more intensively managed for timber production than in the past. However, growth and productivity data are presently limited (Gottfried 1978). Habitat type classifications are recognized for these forests, but little information is available on the timber productivity potential for these habitat types (Moir and Ludwig 1979, Hanks et al. 1983, Alexander et al. 1984). Jones (1974) provides a summary of the silviculture of southwestern mixed conifer forests and emphasizes a need for improving their management based on the application of habitat types or stand types. This study provides additional quantitative data on site potential based on site index measurements for Douglas-fir for several recognized southwestern forest habitat types.

METHODS

Total height and age at diameter breast height were measured for two to six vigorously growing dominant or codominant Douglas-firs in 450 uneven-aged southwestern spruce-fir (31) or mixed conifer (419) stands from 1979 to 1985. Trees with visible signs of abiotic, insect, or disease damage were not selected as site trees in the stands. The following information was recorded for each stand: national forest, location (township, range, and section), elevation (nearest 100 feet), aspect (four cardinal directions), slope (nearest 5%), slope position (flat, bottom, ridge, slope) and

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TABLE 1. Southwestern spruce-fir and mixed conifer habitat types sampled.

Spruce-fir Habitat Types	
ABLA/LIBO:	*Abies lasiocarpa/Linnaea borealis*[2] (*Abies lasiocarpa/Vaccinium scoparium–Linnaea borealis*[4])
ABLA/ EREX:	*Abies lasiocarpa/Erigeron eximius*[2,3] (*Abies lasiocarpa/Erigeron superbus*[4])
Mixed Conifer Habitat Types	
PIEN/SECA:	*Picea engelmannii/Senecio cardamine*[3] (*Picea pungens–Picea engelmannii/Senecio cardamine*[4])
PIEN/EREX:	*Picea engelmannii/Erigeron eximius*[3] (*Picea pungens–Picea engelmannii/Erigeron superbus*[4])
PIPU/EREX:	*Picea pungens/Erigeron eximius*[2,3] (*Picea pungens–Pseudotsuga menziesii*[4])
ABCO/ACGL:	*Abies concolor/Acer glabrum*[1,3] (*Abies concolor–Pseudotsuga menziesii/Acer glabrum*[4])
ABCO/FEAR:	*Abies concolor/Festuca arizonica*[4,5] (*Abies concolor–Pseudotsuga menziesii/Poa fendleriana*[4])
ABCO/QUGA:	*Abies concolor/Quercus gambelii*[1,2,3] (*Abies concolor–Pseudotsuga menziesii/Quercus gambelii*[4])
ABCO/BERE:	*Abies concolor/Berberis repens*[6] (*Abies concolor–Pseudotsuga menziesii*/[sparse][4])
ABCO/EREX:	*Abies concolor/Erigeron eximius*[2,3] (*Abies concolor–Pseudotsuga menziesii/Erigeron superbus*[4])

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TABLE 2. Mean Douglas-fir site indexes and standard deviations by habitat type.

Habitat type	Number of stands	Mean	Site potential class
PIEN/SECA	39	91.3 ± 9.6 A[1]/	High
ABCO/ACGL	69	89.5 ± 11.4 A	High
ABCO/FEAR	25	87.5 ± 8.2 A	High
PIPU/EREX	27	82.6 ± 10.2 B	Moderate
ABCO/EREX	52	81.2 ± 10.8 B	Moderate
ABCO/QUGA	92	76.9 ± 10.7 B	Moderate
PIEN/EREX	28	76.2 ± 17.0 B	Moderate
ABCO/BERE	87	74.5 ± 9.6 B	Moderate
ABLA/EREX	12	73.6 ± 10.7 BC	Moderate
ABLA/LIBO	19	67.3 ± 14.4 C	Low
TOTAL	450		

[1]/ Oneway AOV, $p = 0.10$, Student-Newman-Kuels. Means followed by different letters are significantly different.

habitat type (Moir and Ludwig 1979, Alexander et al. 1984, Fitzhugh et al. unpublished, DeVelice et al. unpublished, Youngblood unpublished). A total of 10 habitat types were sampled (Table 1). Stands sampled were located in the Apache (216 stands), Coconino (9 stands), and Kaibab (23 stands) National Forests, Arizona; the Carson (49 stands), Gil (9 stands), Lincoln (50 stands), and Santa F (58 stands) National Forests, New Mexico and the San Juan National Forest, Colorad (36 stands).

Site indexes were determined from averag height and age data for each stand using th Douglas-fir site index curves developed b Edminster and Jump (1976). Mean site inde and standard deviation were calculated fo each habitat type. A one-way analysis of variance, with $p = 0.10$, was used to compar mean site indexes among habitat types. Th Student-Newman-Kuels test was applied t the analysis to show where significant differences occurred.

RESULTS

The 10 habitat types are divided into thre site potential classes (high, moderate, an low) based on statistically significant differences in mean site indexes (Table 2). Th PIEN/SECA (mean-91.3), ABCO/ACG

(89.5), and ABCO/FEAR (87.6) habitat types are classified as high site potential habitat types for Douglas-fir. The ABLA/LIBO (mean-67.7) is classified as the low potential habitat type. The moderate site potential class includes the remaining six habitat types studied with mean site indexes ranging from 82.6 (PIPU-EREX) to 73.6 (ABLA/EREX). Mean site indexes for the ABLA/EREX and ABLA/LIBO habitat types were not significantly different, but they were classified into different site potential classes because the mean for the ABLA/LIBO habitat type was below 70 feet.

DISCUSSION

Site index is currently the most widely used method of evaluating site quality in the United States (Jones 1969, Husch et al. 1972). Several investigators note significant differences in site index between habitat types for several tree species (Stanek 1966, Roe 1967, Hoffman 1976). However, Daubenmire (1961) rejects the use of ponderosa pine site index curves for predicting potential productivity of habitat types in eastern Washington.

Our results indicate that the southwestern spruce-fir and mixed conifer habitat types sampled in this study can be grouped into three significantly different site quality classes for Douglas-fir. Hoffman (1976) also demonstrates significant differences in Douglas-fir site index between three habitat types in central Idaho.

In their descriptions of southwestern spruce-fir and mixed conifer habitat types, Moir and Ludwig (1979) give estimates of site quality for individual tree species for several habitat types. Their estimates are based on site index and height-age data. Our site index data supports Moir and Ludwig's site quality estimates for Douglas-fir in the PIEN/SECA high potential), PIEN/EREX and PIPU/EREX (moderate potential) and the ABCO/BERE (usually moderate potential) habitat ypes. Our data also confirm their suggestion hat the ABCO/ACGL habitat type has high Douglas-fir height growth potential.

Moir and Ludwig (1979) interpret heights of 75–100 feet in 100 years (breast height age) or the fastest growing Douglas-firs in the ABCO/QUGA habitat type to represent poor o moderate site quality, whereas we interpret these data as representing moderate to high site quality for the Southwest. Our site index data for this habitat type basically correspond to that of Moir and Ludwig's, except the range of site indexes is wider in our study.

Moir and Ludwig (1979) do not present Douglas-fir site quality estimates for three of the habitat types sampled in this study. Based on our site index data, site quality for Douglas-fir is moderate for the ABCO/EREX and ABLA/EREX habitat types and high for the ABCO/FEAR habitat type.

Several investigators discuss the difficulties of using site index for estimating site potential in uneven-aged stands (Stage 1963, Jones 1969, Curtis 1976, Daubenmire 1976). Steele et al. (1981, 1983) use site indexes and normal yield tables to estimate productivity potential for habitat types in Montana and Idaho. However, normal yield tables for Douglas-fir in the Southwest are not available, and we do not feel the use of yield tables from other regions would be valid for the Southwest. The development of separate site curves for different habitat types should improve the accuracy of site index as an estimate of site quality. However, this approach may not solve the problems related to using site index in uneven-aged stands such as early suppression of shade tolerant species (Vincent 1961, Curtis 1976). We agree with the suggestion of Steele et al. (1983) that the development and subsequent validation of growth and yield simulation models using growth coefficients based on habitat types (Stage 1973, 1975) will improve productivity estimates for habitat types.

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WINTERING MULE DEER PREFERENCE FOR 21 ACCESSIONS OF BIG SAGEBRUSH

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ABSTRACT.—Wintering mule deer showed differential browsing preference among 21 accessions of big sagebrush (*Artemisia tridentata*) grown on gardens on three different mule deer herd ranges. The Hobble Creek accession of big sagebrush was significantly preferred over the other 20 accessions across all three sites and for all three years. Accessional preference means for the study period for all sites combined ranged from 28.3 to 57.5%. The data collected support the planned release of the Hobble Creek accession as a superior cultivar of big sagebrush for use on mule deer winter ranges. Plant coumarin content was primarily under genetic control, but site factors also had an effect. Assay for coumarin compounds is useful in determining subspecies of *A. tridentata* but not for precise prediction of mule deer browsing preference.

During in vivo digestion trials Smith (1950) observed that mule deer showed definite aversion to individual big sagebrush (*Artemisia tridentata*) plants. Since then several field workers have observed differential preference of wintering mule deer not only for individual plants but also for populations of big sagebrush (Plummer et al. 1968, Winward 1970, Brunner 1972, Hanks et al. 1973, Stevens and McArthur 1974, Winward and Tisdale 1977, McArthur et al. 1979, Willms et al. 1979). We reported (Welch et al. 1981) that wintering mule deer showed differential preference for 10 accessions of big sagebrush grown on a uniform garden. This study is an effort to include 11 more accessions (21 total), different sites, different mule deer herds, and the role of coumarin compounds in the preference of wintering mule deer for accessions of big sagebrush. Coumarin compounds have been shown to be positively correlated with mule deer preference of some sagebrush taxa (Stevens and McArthur 1974).

MATERIALS AND METHODS

Three outplanting sites were selected within the elevational range of most Utah mule deer winter ranges (1,370–2,140 m): Springville, Utah; 3 km east of Nephi, Utah (Salt Creek Canyon); and 15 km west/southwest of Helper, Utah (Gordon Creek Wildlife Management Area).

The Springville site at 1,402 m is a basin big sagebrush habitat type. Soil is of the Pleasant Grove series (Pleasant Grove gravelly loam, 6–10% slope), consisting of deep, well-drained, gravelly or cobbley soils, alluvial fans. Weathered limestone is the parent material. Soil permeability is moderately rapid. Roots can penetrate to a depth of 1.5 m or more. About 9 cm of available water is held by this soil to a depth of 1.5 m. Soil pH ranges from 7.4 to 7.9. Average annual precipitation is 35–45 cm. The mean annual temperature is 8.9–11.1 C, and the frost-free period is 150–170 days (Swenson et al. 1972).

The Salt Creek Canyon site (1,676 m) is a basin big sagebrush habitat type. Soil is a Rofiss gravelly clay loam 4–15% slope. It is a deep, well-drained alluvial soil. Parent material is Arpien shale. Soil permeability is moderately slow. Effective rooting depth is 1.5 m or more. Soil pH ranges from 8.2 to 8.6. Average annual precipitation is 20–35 cm. The mean annual temperature is 7.2–8.3 C, and the frost-free period is 100–120 days (Soil Conservation Service 1980).

The Gordon Creek Wildlife Management Area, at 2,130 m, is a Wyoming big sagebrush habitat type. Soil is of the Atrac series (Atrac is a very fine sandy loam 1–6% slopes). This series consists of deep, well-drained soils. Parent material is sandstone. Effective rooting depth is 1.5 m or more. Soil pH ranges

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TABLE 1. Locations of collection sites for 21 accessions of big sagebrush (*Artemisia tridentata*) used in this study to determine wintering mule deer preference.

Subspecies	Accession	County and state	Elevation (m)
vaseyana	Colton	Utah, Utah	2,260
	Sardine Canyon	Cache, Utah	1,800
	Benmore	Tooele, Utah	1,900
	Petty Bishop's Log	Sanpete, Utah	2,380
	Durkee Springs	Sevier, Utah	2,270
	Salina Canyon	Sevier, Utah	2,350
	Clear Creek Canyon	Sevier, Utah	2,130
	Pinto Canyon	Washington, Utah	1,850
	Indian Peaks	Beaver, Utah	2,140
	Hobble Creek	Utah, Utah	1,500
tridentata	Clear Creek Canyon	Sevier, Utah	1,720
	Brush Creek	Uintah, Utah	1,830
	Loa	Wayne, Utah	2,140
	Dove Creek	Dolores, Colorado	2,070
	Evanston	Uinta, Wyoming	2,020
	Wingate Mesa	San Juan, Utah	2,060
	Dog Valley	Juab, Utah	1,700
wyomingensis	Evanston	Uinta, Wyoming	2,130
	Kaibab	Coconino, Arizona	2,340
	Trough Springs	Humboldt, Nevada	1,400
	Milford	Beaver, Utah	1,540

from 6.6 to 8.0. Average annual precipitation is 30.5–35.6 cm. The mean annual temperature is 7.2–8.3 C, and the frost-free period is 100–120 days (Soil Conservation Service 1981).

At each site the vegetation was killed by disking and kept weed free by hand and mechanical means. Deer-proof fences were built around each site. We planted each site in spring 1978 with containerized stock of 21 accessions of big sagebrush (Table 1). Each accession was represented by 10 plants, and each plant was an experimental unit within the accessions. The resulting 210 plants in each set were placed at random on a 3 x 3 m grid for each site. Table 1 lists the locations of seed collection sites for the accessions.

We measured the preference for the accessions by randomly selecting 15 annual leaders per plant through the entire crown and measuring them to the nearest centimeter in November 1980, 1981, and 1982. These measurements were used to calculate a mean annual leader length per plant before browsing. We remeasured plants using 15 randomly selected leaders during April 1981, 1982, and 1983 and calculated a mean annual leader length after browsing. Percentage used or preference was calculated by dividing the mean leader length after browsing by the mean leader length before browsing, multiplying by 100, and subtracting from 100. Welch et al. (1981) reported a precision error of 4% for this method. Data were expressed as percentage used (preference).

Ultraviolet visable, fluorescent, water-soluble coumarin compounds (principally isoscopoletin, scopoletin, and esculetin) were measured by placing leaf fragments from single leaves (5 samples/plant) of approximately 1 mg size in water in cuvettes (McArthur et al. 1981). We used 1 mg leaf material/0.3 ml water up to 10 mg leaf material/sample. After 90 minutes equilibration time, spectrophotometric readings (percent transmittance) were made at 364 nm in a Bausch and Lomb Spectronic 700 spectrophotometer. Leaves for coumarin analysis were collected at the time of the 1983 preference measurements.

The three subspecies of big sagebrush, *A. t.* ssp. *tridentata*, *vaseyana*, and *wyomingensis*, were represented in this study. Of the 21 accessions, 10 were *vaseyana*, 7 were *tridentata*, and 4 were *wyomingensis*. This gave the capability of testing for subspecies effects on preference.

Analyses were performed using the SPSS^x statistical package (SPSS Inc., 1983). We used analysis of variance techniques, Student-Newman-Keuls multiple range mean com-

TABLE 2. Effects of subspecies, site, and year on preference of wintering mule deer for accessions of big sagebrush (*Artemisia tridentata*). Data expressed as percent of current year's growth eaten (3 years, 630 plants, three gardens).

	Preference for subspecies	
A. t. ssp. *tridentata*	*A. t.* ssp. *wyomingensis*	*A. t.* ssp. *vaseyana*
32.6^{a*}	35.3^{b}	44.1^{c}
	Effects due to site	
Salt Creek	Gordon Creek	Springville
30.4^{a*}	35.0^{b}	50.2^{c}
	Effects due to years	
1980	1981	1982
31.6^{a*}	41.7^{b}	42.4^{b}

*Means sharing the same superscript are not significantly different at the 5% level.

TABLE 3. Preference of wintering mule deer for accessions of big sagebrush (*Artemisia tridentata*) grown on different gardens. Data expressed as a percent of current year's growth eaten. Data points for gardens represent a three-year mean.

	Garden			
Accession	Gordon Creek	Salt Creek	Springville	Mean
Evanston (t)**	25.2	18.1	41.6	28.3^{a*}
Trough Springs (w)	17.5	30.9	41.9	30.1^{ab}
Dove Creek (t)	26.3	31.3	35.1	30.9^{abc}
Clear Creek Canyon (t)	31.5	19.7	42.7	31.3^{abcd}
Loa (t)	25.0	18.5	51.3	31.6^{abcd}
Kaibab (w)	30.9	27.2	42.4	33.5^{abcd}
Dog Valley (t)	28.6	23.6	49.1	33.8^{abcde}
Brush Creek (t)	35.2	24.6	47.2	35.7^{abcde}
Wingate Mesa (t)	32.5	33.9	42.8	36.4^{abcdef}
Milford (w)	34.9	29.0	47.4	37.1^{bcdefg}
Clear Creek Canyon (v)	34.4	25.6	55.1	38.4^{bcdefg}
Benmore (v)	40.1	39.3	38.4	39.3^{bcdefg}
Pinto Canyon (v)	36.8	27.8	56.2	40.3^{cdefg}
Evanston (w)	31.1	43.8	46.3	40.4^{defg}
Durkee Springs (v)	36.3	27.7	58.1	40.7^{defg}
Salina Canyon (v)	40.5	29.4	55.2	41.7^{efg}
Sardine Canyon (v)	45.8	29.9	58.0	44.6^{fg}
Indian Peaks (v)	40.9	40.9	55.0	45.6^{fg}
Petty Bishop's Log (v)	46.4	33.8	57.7	46.0^{g}
Colton (v)	43.1	37.9	60.1	47.0^{g}
Hobble Creek (v)	52.0	47.4	73.0	57.5^{h}

*Means sharing the same superscript are not significantly different at the 5 % level.
**t = *A. t.* ssp. *tridentata*; v = *A. t.* ssp. *vaseyana*; w = *A. t.* ssp. *wyomingensis*.

parison tests, and regression techniques. Data collected as percent were transformed by the arcsin percentage function for analysis and then returned to the percent values for final presentation (Snedecor and Cochran 1956).

RESULTS AND DISCUSSION

The overall mean percent of leader length used for all years, sites, and accessions was 38.6%. Two three-way analyses of variance detected significant effects due to all main effects of year, site, subspecies, and accession (Table 2).

Wintering mule deer significantly preferred the subspecies *A. t.* ssp. *vaseyana* over *A. t.* ssp. *wyomingensis* and *A. t.* ssp. *tridentata* (Table 2). They significantly preferred *A. t.* ssp. *wyomingensis* over *A. t.* ssp. *tridentata*. These results agree with reports of previous studies (Stevens and McArthur 1974, Welch et al. 1981).

Significantly more big sagebrush was consumed by wintering mule deer at the Springville site than at Salt Creek and Gordon Creek (Table 2). Big sagebrush consumption was significantly more at Gordon Creek than at Salt Creek. This differential use among the sites strengthens our ability to rank the pref-

TABLE 4. Analysis of variance of amount of coumarin by subspecies and effects due to site. Data are presented as percent transmittance (364 mm)*.

Amount of coumarin by subspecies*		
A. t. ssp. *tridentata*	*A. t.* ssp. *wyomingensis*	*A. t.* ssp. *vaseyana*
61.9^{a**}	54.7^{b}	37.7^{c}
Effects due to site**		
Salt Creek	Gordon Creek	Springville
43.6^{a***}	48.6^{b}	57.9^{c}

*Percent transmittance is an inverse function of coumarin content.

**Means sharing the same superscript are not significantly different at the 5% level.

***Springville site differences were compounded by disproportionate mortality of ssp. *vaseyana* prior to 1983 at that site.

TABLE 5. Linear regression comparisons of mean preference and percent transmittance values.*

Comparison	Number of pairs	r	Significance
All accessions	21	− 0.58	.01
Subspecies	3	− 0.998	.05
A. t. ssp. *tridentata*	7	− 0.75	ca. .05
A. t. ssp. *wyomingensis*	4	+ 0.82	NS
A. t. ssp. *vaseyana*	11	+ 0.01	NS

*Values computed from Tables 2 and 4 using mean values only (Snedecor and Cochran 1956). Percent transmittance is an inverse function of coumarin content.

erence of mule deer for the accessions of big sagebrush. Also, different mule deer herds occupied the three sites, thus eliminating any confounding resulting from previous exposure to a given type of big sagebrush.

Significantly more big sagebrush was consumed during 1981 and 1982 than in 1980 (Table 2). We have no explanation for these differences.

Wintering mule deer significantly preferred the Hobble Creek accession over the other 20 accessions across all sites and years (Table 3). Overall use of the Hobble Creek accession was 57.5%. Use of Hobble Creek big sagebrush varied significantly between sites. At the Salt Creek site, the Hobble Creek accession received 47.4% use, 52.0% use at Gordon Creek, and 73.0% use at Springville. The consistency of ranking for preference of the Hobble Creek accessions was not present for the other accessions and further strengthens our contention that the Hobble Creek is the most preferred. This consistency was also true for years. These study results agree with our earlier study (Welch et al. 1981). We are currently collecting data needed to support the release of Hobble Creek through the Soil Conservation Service plant development program as a superior cultivar of big sagebrush for use on mule deer winter ranges.

Different levels of coumarin compounds were found to be present in each subspecies (Tables 4 and 5). Earlier studies have shown that ssp. *vaseyana* had higher coumarin levels than ssp. *tridentata* and *wyomingensis* (Stevens and McArthur 1974, McArthur et al. 1981). In a previous report, we suggested that these coumarin compounds would be useful for indirect selection for preference (Welch and McArthur 1979). This study shows that there is an environmental component to coumarin content (Table 4). The effects due to site are significant. Nevertheless, genetic factors are of overriding importance. Subspecies were significantly different in coumarin content (Tables 4 and 5), and individual accessions ranked rather consistently in coumarin content across sites (Table 6). Coumarin content data from a set of plants over three years and all seasons showed that, whereas coumarin levels may vary temporally, individual plants maintain general positions in respect to other plants in the population (McArthur, Welch, and Noller, data on file, Shrub Sciences Laboratory).

Coumarin compounds are useful indicators of *A. tridentata* subspecies—especially in distinguishing ssp. *vaseyana* from ssp. *tridentata* and *wyomingensis* (Stevens and McArthur 1974, McArthur et al. 1981, Table 4). Their use as preference indicators for browsing

TABLE 6. Percent transmittance at 364 nm by accession and site. Mean preference* is also given.

		Percent transmittance			
Accession	Mean preference	Gordon Creek	Salt Creek	Springville	Mean
Dove Creek (t)**	30.9	63.0	62.9	72.9	66.1^{a}***
Clear Creek Canyon (t)	31.3	66.9	57.2	68.6	63.9^{ab}
Evanston (t)	28.3	57.0	63.8	69.0	63.4^{ab}
Dog Valley (t)	33.8	67.7	58.4	63.7	63.3^{ab}
Loa (t)	31.6	63.4	58.0	67.5	62.8^{ab}
Evanston (w)	40.4	67.2	56.9	52.6	59.3^{abc}
Wingate Mesa (t)	36.4	58.2	53.9	64.5	58.9^{abc}
Brush Creek (t)	35.7	64.3	49.3	49.0	54.6^{bcd}
Milford (w)	37.1	57.5	46.8	57.1	53.7^{bcd}
Pinto Canyon (v)	40.3	49.4	49.4	63.2	53.7^{bcd}
Trough Springs (w)	30.1	57.7	50.0	51.5	53.0^{bcd}
Kaibab (w)	33.5	49.1	51.9	53.5	52.6^{bcd}
Hobble Creek (v)	57.5	49.5	45.3	56.5	49.5^{cd}
Colton (v)	47.0	47.3	40.8	48.2	45.5^{d}
Indian Peaks (v)	45.6	46.1	41.4	53.1	34.2^{d}
Durkee Springs (v)	40.7	44.2	37.1	57.4	45.0^{d}
Clear Creek Canyon (v)	38.4	29.1	26.0	53.0	33.1^{e}
Sardine Canyon (v)	44.6	23.4	22.6	55.0	31.6^{e}
Salina Canyon (v)	41.7	21.7	28.4	48.2	31.2^{e}
Benmore (v)	39.3	26.0	16.8	43.5	27.1^{e}
Petty Bishop's Log (v)	46.0	16.4	13.4	****	14.8^{f}

*From Table 3.

**t = *A. t.* ssp. *tridentata*; v = *A. t.* ssp. *vaseyana*; w = *A. t.* ssp. *wyomingensis*.

***Means sharing the same superscript are not significantly different at the 5% level.

****No surviving plants in 1983.

mule deer is examined in Tables 5 and 6. We concluded that these compounds are good general indicators in the sense that the subspecies are browsed differentially by mule deer (Table 2), and those differences are reflected by differences in coumarin content (Table 4). The relationship is ssp. *vaseyana* > ssp. *wyomingensis* > ssp. *tridentata* in browsing preference and in coumarin content. However, the relationship of coumarin content to browsing preference is not strong nor consistent within subspecies (Tables 5 and 6). A regression analysis (SPSS^{x}) interacting all (n=573) coumarin and preference data points gave an unimpressive but highly significant ($p < .001$) r^2 of 0.06. Linear regression values were strikingly different in magnitude and sign for the three subspecies (Table 5). Furthermore, an examination of the data for the most preferred accession, Hobble Creek (ssp. *vaseyana*), shows that it has a relatively low coumarin content for its subspecies (Table 6). Coumarin content is useful in identifying preferred taxa but not in making distinctions within those taxa.

The chromosome number level may impact coumarin content. Most ssp. *tridentata* and *vaseyana* accessions are diploid. The *wyomingensis* accessions are tetraploid (McArthur et al. 1981, McArthur and Welch 1982). Both tetraploid spp. *tridentata* accessions (Wingate Mesa and Brush Creek) are relatively high in coumarin content (Table 6). Two of the ssp. *vaseyana* accessions with relatively low coumarin content (Colton and Pinto Canyon) are tetraploid. The additional genomes may be responsible for a moderating effect in the case of tetraploids for both ssp. *tridentata* and *vaseyana*. Tetraploid plants of both subspecies move toward intermediate values from the more extreme values of their respective diploids.

ACKNOWLEDGMENTS

The authors acknowledge the excellent technical assistance of Tracy Jacobson. They also acknowledge cooperative arrangements with the Utah Division of Wildlife Resources in obtaining plant materials and maintenance of the Springville and Gordon Creek sites (Central Regional Office and the Pittman-Robertson Wildlife Restoration Funds, Project W-82-R).

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COLEOPTERA OF THE IDAHO NATIONAL ENGINEERING LABORATORY: AN ANNOTATED CHECKLIST

Michael P. Stafford[2], William F. Barr[2] and James B. Johnson[2]

Abstract.—An insect survey was conducted on the Idaho National Engineering Laboratory during the summers of 1981–1983. This site is on the Snake River Plains in southeastern Idaho. Presented here is an annotated checklist of the Coleoptera collected. Successful collecting methods, dates of adult occurrence, and relative abundance are given for each species. Relevant biological information is also presented for some species.

The Idaho National Engineering Laboratory (INEL) was designated an Environmental Research Park in 1975. Because of the increased number of ecological studies on the INEL since this time, there is a need for an entomofaunal list for this area. This information will be valuable to many biologists since insects interact with many other organisms, e.g., plants as pollinators and herbivores or vertebrates as food and parasites. Therefore, an insect survey was conducted on the INEL during the summers of 1981–1983. The objectives of this survey were to document the taxonomic composition of the insect fauna and the seasonal occurrence, relative abundance, and host information for the insect species present.

Several arthropod surveys were conducted on the INEL, formerly known as the National Reactor Testing Station, under the auspices of Brigham Young University. Allred (1968) reported seven species of ticks from a variety of hosts. Forty-two species of spiders were collected in a pitfall trap survey (Allred 1969). Allred and Cole (1971) published a checklist of 22 species of ants, and Allred and Muma (1971) listed the solpugid species found on the INEL. Allred (1973) reported the occurrence of scorpions. Although these studies provide valuable information on the ant and arachnid faunae, information on other insect taxa is lacking.

Study Area

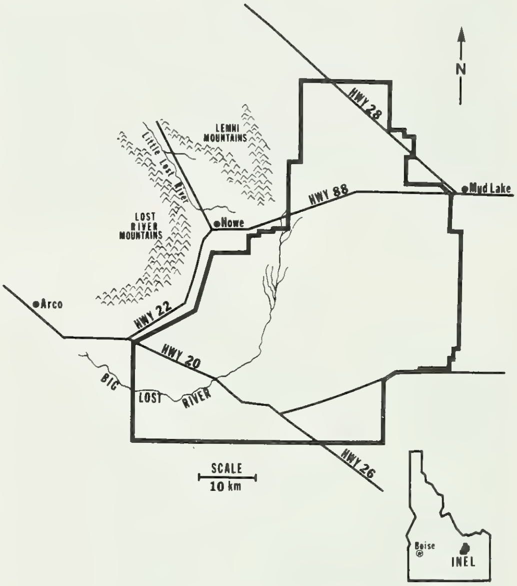

Fig. 1. Location and detail of the Idaho National Engineering Laboratory.

The INEL is on the Upper Snake River Plains at the base of the Lost River and Lemhi Mountain Ranges in southeast Idaho (Fig. 1). The topography is flat to gently rolling; mean elevation is 1,490 m. Soils are generally aeolian sandy loams and loess and classified as Aridisols (McBride et al. 1978), with scattered lava outcroppings. The vegetation is dominated by big sagebrush (*Artemisia tridentata* Nutt.) Other conspicuous shrubs include green rabbitbrush (*Chrysothamnus viscidifloris* [Hook.] Nutt.), gray rabbitbrush (*C. nauseosus* [Pall.] Britt.), gray horsebrush (*Tetradymia canescens* D.C.), and winter fat

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[1] Published with the approval of the director of the Idaho Agriculture Station as Research Paper 85724.

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(*Ceratoides lanata* [Pursh] J. T. Howell). The dominant grasses are bluebunch wheatgrass (*Agropyron spicatum* [Pursh] S. & S.), Indian ricegrass (*Oryzopsis hymenoides* [R. & S.] Ricker), bottlebrush squirreltail (*Sitanion hystrix* [Nutt.] J. B. Smith), and needle-and-thread (*Stipa comata* Trin. & Rupr.). The more alkaline areas are dominated by shadscale (*Atriplex confertifola* [Torr. & Frem.] Wats.) and saltsage (*A. nuttalii* Wats.). In depressions prone to flooding are stands of Great Basin wildrye (*Elymus cinereus* Scribn. & Merrill). Extensive stands of Utah juniper (*Juniperus osteosperma* [Torr.] Little) occur on the foothills of the surrounding mountains. Harniss and West (1973) described the vegetation patterns and presented a detailed map of the vegetation found on the INEL. Jeppson and Holte (1978) listed the plant species found in the area.

RESULTS

Presented here is an annotated checklist of the Coleoptera we collected in approximately 800 man-hours of collecting during this survey and previous collecting efforts on the INEL over the last 25 years by one of us (WFB). The list includes 214 species in 29 families, making it the most extensive faunal list yet published for the INEL. This information should be useful for those undertaking entomological and ecological studies in semiarid regions of the West, particularly in the Great Basin and Snake River Plains. The placement of family names follows *A Catalog of the Coleoptera of America North of Mexico* (Kingsolver 1979). Genus and species names are arranged in alphabetical order. Determinations, except as noted in the acknowledgments, were made by the authors and Paul J. Johnson (also at the University of Idaho) using published keys, e.g. Arnett (1963) and Hatch (1953–1973), and the University of Idaho insect collection as reference material. Following each species are the collecting methods, dates of occurrence, and abundance. Biological information is presented for some species. Voucher specimens are housed in the William F. Barr Entomological Museum at the University of Idaho.

Collecting Methods

BF = Berlese Funnel; GC = General Collecting; LT = Light Trap; MT = Malaise Trap; SW = Sweep Net; PE = Plant Examination; PF = Pitfall Trap; WP = Windowpane Trap.

Relative Abundances

U = Uncommon, 1–15 specimens; C = Common, 16–50 specimens; A = Abundant, 51+ specimens.

The assignment of the abundance rating is subjective. It is based upon both the number of specimens collected and on personal observations. Because of population fluctuations we have observed over the years, these ratings may not always be indicative of the abundance of a species in that particular year. Also, the collecting methods employed may not always reflect the relative abundance of a species.

COLEOPTERA CHECKLIST

Carabidae

Agonum balesi Gray: PF; May, Jun; U.
Agonum placidum (Say): LT; Jul; U.
Amara apricaria Paykull: LT; Jul; U.
Amara impuncticollis Say: PF; Jul; U.
Amara laticollis LeConte: LT; Jul; U.
Amara musculus Say: PF; Jun, Jul; U.
Amara sp. (poss. *quenseli* Schonherr): PF; Jul; U.
Axinopalpus biplagiatus (Dejean): PF, WP; Jul; U.
Bembidion immaculosum Hatch: LT, PF; Jul, Aug; U.
Bembidion nebraskense LeConte: LT; Aug; U.
Bembidion obscurellum Motschulsky: LT; Jul, Aug; A.
Bembidion rupicola Kirby: LT; Aug; U.
Bembidion timidum LeConte: LT; Aug; U.
Calosoma luxatum Say: PF; May–Jul; U.
Cicindela decemnotata Say: PF, GC; May–Aug; U.
Cymindis planipennis LeConte: PF; Jun–Aug; U.
Harpalus amputatus Say: PF; May; U.
Harpalus basilaris Kirby: PF; Jun; U.
Harpalus fraternus LeConte: LT, PF; Jun, Jul; U.
Lebia vittata (Fabricius): WP; May–Jul; U.
Microlestes nigrinus (Mannerheim): PF; Jun, Jul; U.
Philophuga viridis Dejean: PF, PE; May–Jul; U. Larva observed feeding on larva of the sagebrush defoliator, *Aroga websteri* Clark, (Lepidoptera: Gelechidae), on *A. tridentata*.

Piosoma setosa LeConte: PF, WP; Jun, Jul; U. New state record.
Pseudomorpha behrensi Horn: PF; Jul, U.

Dytiscidae

Laccophilus decipiens LeConte: LT; Aug; U.

Hydrophilidae

Berosus fraternus LeConte: LT; Jul; U.
Berosus styliferus Horn: LT; Jul, Aug; U.
Cercyon quisquilius (Linnaeus): LT; Jul; U.
Helophorus sp.: LT; Jul, Aug; U.
Sphaeridium scarabaeoides (Linnaeus): PF; Jun–Aug; U.

Histeridae

Psiloscelis corrosa Casey: WP; Jun; U. New state record.
Saprinus lugens Erichson: GC; May; U.
Saprinus oregonensis LeConte: PF; Jun, Jul; U.
Xerosaprinus acilinea (Marseul): PF; Jun, Jul; U.
Xerosaprinus lubricus (LeConte): PF; Jun–Aug; C.

Scarabaeidae

Aphodius denticulatus Haldeman: LT, PF; May–Jul; U.
Aphodius distinctus Müller: PF; May; U.
Aphodius fossor (Linnaeus): GC; Jul; U.
Aphodius hirsutus Brown: PF; May; U.
Aphodius granarius (Linnaeus): PF; Jun; U.
Aphodius vittatus Say: PF; Jul; U.
Aphodius sp. (poss. *militaris* LeConte): PF, WP; May; U.
Boreocanthon simplex (LeConte): PF; May; U.
Cremastocheilus crinitus bifoviatus Van Dyke: PF, GC; Jun, Jul; U.
Dichelonyx truncata LeConte: GC; Jun, Jul; C.
Diplotaxis haydenii LeConte: GC, LT, WP; Jun, Jul; U.
Diplotaxis obscura LeConte: PF; May–Aug; C.
Diplotaxis subangulata LeConte: LT, WP; Jul; U.
Glaresis canadensis Brown: PF; Jun–Aug; C.
Ochodaeus simplex LeConte: LT, WP; Jul, U.
Paracotalpa granicollis (Haldeman): GC; Jul; U.
Serica anthracina LeConte: GC, PF; Jun; U.
Serica barri Dawson: LT, PF; Jul; A.
Trox sp.: LT; Jun; U.

Leiodidae

Hydnobius sp.: LT, PF; Jun, Jul; U.
Ptomophagus californicus (LeConte): PF; Jul; U.

Silphidae

Nicrophorus hecate Bland; PF, WP; May–Aug; C.

Staphylinidae

Anotylus sp.: LT; Aug; U.
Bledius strenuus Casey: LT; Jul; U.
Philonthus concinnus (Gravenhorst): PF; May; U.
Philonthus cruentatus (Gmelin): PF; May; U.
Platystethus americanus (Erichson): LT; Aug; U.
Tachinus angustatus Horn: WP; Jun; U.

Pselaphidae

Pilopius sp.: GC; May; U.

Heteroceridae

Lanternarius brunneus (Melsheimer): LT; Jun; U.

Buprestidae

Acmaeodera immaculata Horn: GC, PE; Jul; C. Larvae bore roots of *C. lanata*, adults on flowers of *Opuntia polyacantha* Haw.
Agrilus politus (Say): GC, PE; Jul–Aug; U. Larvae bore *Salix* spp.
Agrilus pubifrons Fisher: GC, PE, SW; Jul, Aug; C. Larvae bore roots and adults feed in the flowers of *C. viscidifloris*.
Agrilus walsinghami Crotch: GC, PE; Aug; U. Larvae bore roots of *C. nauseosus*.
Anthaxia retifer LeConte: GC, PE; May; U. Adults on flowers of *Balsamorhiza sagittata* (Pursh) Nutt.
Chrysobothris deleta LeConte: GC, PE; Aug; U. Larvae bore roots of *A. tridentata*.
Chrysobothris horningi Barr: GC, PE; May; U. Larvae bore roots of *Eriogonum* spp.
Chrysobothris idahoensis Barr: GC, PE; Jun–Aug; U. Larvae bore roots of *Eriogonum* spp.
Chrysobothris texana LeConte: GC, PE; Jun–Aug; C. Larvae bore branches of *J. osteosperma*.
Nannularia brunneata (Knull): GC, PE; Jul; U. Larvae bore roots of *Eriogonum* sp.

Elateridae

Ampedus ursinus (Van Dyke): PF; Jun; U.
Anchastus cinereipennis (Ecshscholtz): PF; May–Jul; C. Adults associated with *E. cinereus.*
Cardiophorus sp. 1: BF, PF; Mar, May, Jun; U.
Cardiophorus sp. 2: PF; May, Jun; U.
Cardiophorus sp. 3: GC, PF; May, Jun; U.
Cardiophorus sp. 4: WP; Jun; U.
Cardiophorus sp. 5: BF, PF, WP; Mar, May; U.
Ctenicera noxia (Hyslop): PF; May, Jun; U.
Ctenicera semivittata (Say): GC; May; U.
Hypolithus bicolor (Eschscholtz): PF; Jul; U.

Cantharidae

Malthodes sp.: GC; May, U.

Dermestidae

Dermestes marmoratus Say: GC, LT; Jul, Aug; C.

Cleridae

Enoclerus acerbus Wolcott: GC, PF, WP; May–Jul; C.
Enoclerus barri Knull: GC; Jul, Aug; U.
Phyllobaenus sp.: GC, PE, SW, WP; Jun–Aug; C. Adults often found on *A. tridentata* preying on small Lepidoptera larvae.
Trichodes ornatus Say: WP; Jul; U.

Melyridae

Amecoceris spp.: BF, PF, WP; May–Jul; A.
Attalus glabrellus Fall: GC, WP; May–Jul; C.
Attalus morulus smithi Hopping: GC, SW; May, Jun; U. Adults associated with *E. cinereus.*
Attalus oregonensis Horn: GC, PE, PF; Jun, Jul; C. Adults feed on pollen in flowers of *O. polyacantha.*
Collops bipunctatus (Say): PE, SW; Jul; U. Adults feed on pollen of *E. cinereus.*
Collops bridgeri Tanner: GC, PF; May–Jul; U.
Collops hirtellus LeConte: SW; Jun; U.
Collops punctulatus LeConte: PF, WP; U.
Dasytellus sp.: PF, WP; Jul; C.
Hoppingiana nitida Hatch: WP; Jul; U.
Trichochrous spp.: GC, PE, WP; C. Adults feed on pollen in flowers of *O. polyacantha.*

Nitidulidae

Brachypterolous pulicarius (Linnaeus): WP; Jul; U.
Carpophilus pallipennis (Say): GC, PE, WP; Jun–Aug; C. Adults feed on pollen in flowers of *O. polyacantha.*

Phalacridae

Olibrus rufipes LeConte: GC, PE; Aug; C. Adults feed on pollen in flowers of *C. viscidifloris.*
Phalacrus penicillatus Say: GC, PE, SW; U. Adults associated with *E. cinereus.*

Coccinellidae

Brachyacantha dentipes socialis Casey: GC; Aug; U.
Brachyacantha ursina uteella Casey: GC, SW; Jun, Jul; U.
Brumus septentrionus Weise: GC; Jun–Aug; U.
Coccinella difficilis Crotch: WP; May, Jun; U.
Coccinella novemnotata degener Casey: SW; Aug; U.
Coccinella prolongata Crotch: WP; Jun; U.
Coccinella transversoguttata richardsoni Brown: GC, LT; May–Aug; U.
Hippodamia apicalis Casey: GC, SW, WP; Jun–Aug; A.
Hippodamia convergens Guerin: SW; May–Aug; U.
Hippodamia glacialis lecontei Mulsant: WP; Aug; U.
Hippodamia quinquesignata Kirby: GC; May; U.
Hippodamia tredecimpunctata tibialis (Say): LT; Aug; A.
Hyperaspidius hercules Belicek: PF, WP; Jun–Aug; U.
Hyperaspidius vittigera LeConte: WP; Aug; U.
Hyperaspis lateralis montanica Casey: MT, SW, WP; May–Aug; U.
Nephus sordidus (Horn): PF; Jun; U.
Scymnus caurinus Horn: SW; Jun; U.
Scymnus marginicollis Mannerheim: PF, WP; Jun–Aug; U.
Scymnus postpictus Casey: WP; Jul; U.

Lathridiidae

Melanopthalma americana Mannerheim: BF; May; U.
Melanopthalma sp.: SW; Jul; U.

Tenebrionidae

Alaudes singularis Horn: BF; Mar; U.
Araeoschizus airmeti Tanner: GC, PF; May–Aug; U. Inquiline in the nests of the harvester ant, *Pogonomyrmex owhyheei* Cole
Blapstinus barri Boddy: PF, WP; May, Jun; U.
Blapstinus substriatus Champion: PF, WP; May–Jul; C.
Coelocnemis punctatus LeConte: PF; Aug; U.
Coniontis obesa LeConte: PF; May, Jun; U.
Coniontis setosa Casey: BF, PF; Mar, May, Jun; U.
Eleodes cordata Eschscholtz: PF; May–Aug; U.
Eleodes extricata cognata Haldemann: GC, PF; May–Aug; A.
Eleodes hispilabris connexa LeConte: PF; May–Jul; U.
Eleodes nigrina LeConte: GC; Jul, Aug; U.
Eleodes obscura Say: PF; May–Aug; U.
Eleodes pilosa Horn: GC, PF; May–Aug; A.
Embaphion elongatum Horn: PF; May–Jul; U.
Helops californicus Mannerheim: PF; May, Jun; U.
Helops convexulus LeConte: BF; Mar; U.
Helops opacus LeConte: PF; May–Jul; U.
Melanastus ater (LeConte): BF, PF, Mar, Jul; U.
Oxygonodera hispidula (Horn): PF; May–Aug; C.
Sphaeriontis muricata (Casey): PF; Jun; U.

Alleculidae

Mycetochara procera Casey: GC, WP; May, Jun; U.

Oedemeridae

Oxacis bicolor (LeConte): WP; Jul; U.

Mordellidae

Mordellistena idahoensis Ray: PF; Jun; U.
Mordellistena sericans Fall; MT, WP; Jun, Jul; U.

Meloidae

Epicauta immerita Walker: WP; Jun; U.
Epicauta piceiventris Maydell: WP; Jul; U.
Gnathium eremicola Macswain: GC, PE; Aug; A. Adults feed on nectar in flowers of *C. viscidifloris*.
Lytta vulnerata cooperi LeConte: GC, PE; Aug; U.
Nemognatha lutea LeConte: GC; Jun; U.

Anthicidae

Anthicus cervinus LaFerté: LT; Aug; U.
Anthicus formicarius LaFerté: PF; Jul; U.
Anthicus hastatus Casey: LT; Aug; U.
Notoxus serratus LeConte: GC, PE, PF, WP; May–Jul; C. Adults feed on pollen and developing seeds of *E. cinereus*.

Cerambycidae

Centrodera nevadica nevadica LeConte: LT, PF, WP; Jul, Aug; C.
Cortodera barri Linsley & Chemsak: GC, MT, PE, PF, WP; Jun; U. Adults associated with *E. cinereus*.
Crossidius ater LeConte: GC, PE; Aug, Sep; U. Larvae bore roots of *A. tridentata*.
Crossidius coralinus LeConte: GC, PE; Aug; U. Larvae bore roots and adults feed on pollen of *C. nauseosus*.
Crossidius hirtipes allgewahri LeConte: GC, PE; Aug; U. Larvae bore roots and adults feed on pollen of *C. viscidifloris*.
Crossidius punctatus LeConte: GC, PE; Aug, Sep; U. Larvae bore roots and adults feed on pollen of *C. nauseosus*.
Judolia gaurotoides Casey: GC, PF; May; U.
Mecas bicallosa Martin: PE; Jun; U. Larvae bore roots of sagebrush.
Megacheuma brevipennis (LeConte): GC, PE; Aug; C. Larvae bore roots of *A. confertifolia, A. nuttali,* and *Sacrobatus vermiculatus* (Hook.) Torr.
Megasemum asperum (LeConte): LT; Jul; U.
Prionus californicus Motschulsky: GC; Aug; U.

Bruchidae

Acanthoscelides pauperculus (LeConte): GC, WP; Jun–Aug; U.

Chrysomelidae

Altica sp.: GC; Jun; U. Adults associated with *E. cinereus*.
Anisostena californica Van Dyke: GC; Aug; U. Adults associated with *E. cinereus*.
Brachycoryna montana (Horn): GC; Jul; U.
Chaetocnema sp.: PF; Jun, Jul; U.
Crepidodera nana (Say): GC; Jun; U.
Cryptocephalus spurcus LeConte: GC, SW; Jul; U. Adults and larvae feed on foliage of *C. viscidifloris*.
Disonycha latifrons Schaeffer: PF, SW; May–Aug; C. Larvae and adults feed on foliage of *C. viscidifloris*.

Exema conspersa (Mannerheim): SW; Jul, Aug; U.

Glyptoscelis sp. (poss. *artemisiae* Blake): PF, SW, WP; May, Jun; U.

Monoxia consputa LeConte: PF, SW, WP; May, Jun; U.

Monoxia pallida Blake: WP; Jul; U.

Monoxia puberula Blake: GC; Jul; U.

Pachybrachys caelatus LeConte; PE, SW; Jun–Aug; C. Feeds on foliage of *C. viscidifloris.*

Pachybrachys jacobyi Bowditch: GC; Jun–Aug; U.

Phyllotreta albionica LeConte: PF, SW; May–Aug; C. Adults commonly found on wild mustards, *Descurania* spp. and *Schoenocrambe linifolia* (Nutt.) Greene.

Pyrrhalta luteola (Müller): GC; Jul; U.

Pyrrhalta nymphaeae (Linnaeus): GC; Jun; U.

Saxinis saucia LeConte: GC; Jul; U.

Scelolyperus nigrovirescens (Fall): GC; Jun; U.

Stenopodius vanduzeei Blaisdell: GC; Jul; U.

Systena blanda (Melsheimer): GC; Jul; U.

Trirhabda nitidicollis LeConte: GC, PE, Jul; C. Adults and larvae feed on *C. nauseosus.*

Anthribidae

Trigonorhinus sp. (near *annulatus* Carr): WP; Jun, Jul; U.

Curculionidae

Acmaegenius granicollis Van Dyke: GC; Jun; U.

Anthonomus sp. 1: GC, PE, SW; Jun–Aug; U. Adults feed on foliage of *C. viscidifloris.*

Anthonomus sp. 2: GC, PE, SW; Jun–Aug; C. Adults feed on foliage of *C. viscidifloris*.

Apion sordidum Smith: PE, PF, SW, WP; May–Jul; U. Inquiline in tephritid and cecidomyiid galls on *A. tridentata.*

Brachyrhinus ovatus (Linnaeus): GC; Jun–Aug; U.

Cleonus kirbyi Casey: PF; May, Jun; U.

Cleonus quadrilineatus (Chevrolat): PF; May, Jun; U.

Cosmobaris americana Casey: MT; Jun; U.

Dinocleus denticollis Casey: PF; May, Jun; U.

Dyslobus alternatus Horn: PF; May–Aug; C.

Gyrotus sinuatus Hatch: PE; Jul; U. Larvae bore in *Artemisia* stems.

Miloderoides maculatus VanDyke: PF; Jun, Jul; U.

Myrmex vittatus (Horn): GC; Jul, aug; U.

Ophryastes latirostris LeConte: GC, PE; Jun; U. Larvae and adults feed on foliage of *C. lanata.*

Sitona hispidula (Fabricius): LT; Aug; U.

Smicronyx sp.: PF; SW; Jun–Aug; U.

Sphenophorus gentilis LeConte: PE, PF, SW; May–Jul; A. Adults feed on developing seed heads of *E. cinereus*.

Trachyphloeni sp. (undescribed genus): PF; Jul, Aug; U.

Tychius tectus LeConte: PF; June; U.

ACKNOWLEDGMENTS

Appreciation is extended to the following persons for the identification of specimens: R. S. Anderson, University of Alberta (Curculionidae: *Cleonus*); A. F. Newton, Museum of Comparitive Zoology—Harvard University (Staphylinidae); R. L. Penrose, California Department of Agriculture (Cerambycidae: *Centrodera*); C. A. Triplehorn, Ohio State University (Tenebrionidae: *Coniontis*); R. L. Wenzel, Field Museum of Natural History—Chicago (Histeridae); and D. R. Whitehead, Systematics Entomology Laboratory, USDA (Curculionidae: Trachyphloenini). We thank O. D. Markham, U.S. Department of Energy, and Frank Merickel, University of Idaho, for their help and support. This work was conducted for the INEL Radioecology and Ecology Programs sponsored by the Office of Health and Environmental Research, United States Department of Energy.

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MICROHABITAT AFFINITIES OF GAMBEL OAK SEEDLINGS

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ABSTRACT.—Previous work suggested that Gambel oak seedlings are rare in the northern parts of its range in Utah where summer rainfall is relatively low but should be abundant in southern parts of the range where summer rainfall is usually high. Gambel oak grades from a relatively minor component of a ponderosa pine/mixed conifer assemblage in the south to a virtually monotypic formation in the north, where it exists as long-lived clones.

Quadrat analysis in Arizona and New Mexico, within the oak zone, revealed a seedling density ranging from 120 to 1320 per hectare. We found a significant tendency of seedlings to be located on the NE (cool, shady) side of sheltering objects in the environment. Mature ponderosa pine ranged in density from ca 40 to 500 stems per hectare, whereas mature Gambel oak ranged from ca 10 to 20 genets per hectare with ca 1 to 7 ramets per clone. These results support our previous conclusion that Gambel oak in northern Utah probably became established as a minor component of a mixed pine/oak woodland at a time in mid-Holocene when summer rainfall was much higher than today.

Gambel oak (*Quercus gambelii* Nutt.), a deciduous, white oak, is the dominant oak of the southern Rocky Mountain region. Its distribution is primarily encompassed by the states of Utah, Colorado, Arizona, and New Mexico. We previously demonstrated that the northern limits of Gambel oak in Utah appear to be constrained by the combined effects of two distinct airmass gradients (Neilson and Wullstein 1983). Probabilities of late spring freeze as determined by the polar front gradient and summer drought as determined by the "Arizona Monsoon" gradient appear to covary during global warming and cooling trends and appear to have synergistically produced a relatively sharp northern boundary (Neilson and Wullstein 1983). At present, seedling establishment of Gambel oak is rare in the northern part of its range (Neilson and Wullstein 1983). Our transplant studies (seeds and seedlings, Neilson and Wullstein 1983) and physiological studies (Neilson and Wullstein 1986) indicate that natural seedling establishment may be expected to occur only in the parts of the range where summer rains are sufficient for seedling survival.

Gambel oak persists at its northern limits today by virtue of rhizomatous, asexual reproduction (Neilson and Wullstein 1983). We believe that these oaks became established at their northern limits through sexual reproduction and seed dispersal at some time during the mid-Holocene thermal maximum when limiting stresses would have been reduced (Neilson and Wullstein 1983). At that time the shrub and tree community composition in northern Utah, near the northern limits of distribution for this species, might have been similar to that where the species is capable of sexual reproduction and seedling establishment today. Near its northern limits today, where it reproduces asexually, Gambel oak forms an essentially monotypic plant formation, or "mountain brush community" (Ream 1963). In the southern part of its range, where it reproduces sexually, Gambel oak is a relatively minor component of a mixed pine-oak woodland. The purpose of this study is to document the density of Gambel oak seedlings in regions of high summer rainfall, their microhabitat affinities and the general canopy composition of their associated plant communities.

METHODS

In September 1979, 15 quadrats were established in Arizona and New Mexico to ascertain the density of Gambel oak seedlings in various habitats. Excavation of root systems revealed that seedlings can usually be distinguished from suckers on the basis of clustering. Suckers tend to occur in tight clusters, while seedlings are widely dispersed. In many cases the spent acorn was still attached to the seedling. It was also found that true seedlings possessed a readily extractable, vertically oriented taproot, which exhibited well-defined taper, whereas suckers were always attached to a horizontally oriented rhizome within a few cm of the surface, which exhibited little or no taper. Thereafter, seedlings were distinguished from suckers by counting shoots that exhibited isolation from other shoots by more than two meters. In doubtful instances plants were examined for tap roots. All oaks less than 30 cm in crown height were arbitrarily classified as seedlings unless otherwise determined to be suckers. Fourteen large seedlings were collected at random for estimations of age and taproot growth rates.

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Of the 15 quadrats, 13 were 0.1 ha and square. The remaining two quadrats were 0.04 and 0.05 ha, respectively, and roughly square. The quadrat sites were chosen to reflect apparent extremes of habitat within an area. In areas exhibiting little variation in topography (e.g., two flat sites south of Flagstaff), the quadrat placement was essentially random. In areas of diverse topography, the quadrats were chosen to encompass previous seedling plantings (Neilson and Wullstein 1983), selected to reflect mesic and xeric extremes within the region.

Three quadrats were placed in each of two flat sites on the Mogollon Rim south of Flagstaff near the headwaters of Oak Creek Canyon. Three contiguous quadrats on Humphrey Peak (near Flagstaff, Arizona) sampled a gradient from swale to ridge on an east-facing slope. Three quadrats were established in the vicinity of Pinedale, Arizona, on the Mogollon Rim. Two of these were on flats separated by several kilometers. The third was on a south-facing slope. There were no previous plantings in this vicinity. Three quadrats were placed in the Sandia Mountains of New Mexico. Two of these were on east-facing ridges of differing moisture regime located near Cold Spring Picnic Ground (see Table 1). The third was on a southfacing slope. Latitude, longitude, elevation, slope, aspect, general canopy composition and density were noted. These data are summarized in Table 1.

As the natural seedlings were counted, they were marked with orange paint to eliminate double counting and to insure a complete count. The location of each seedling was noted with regard to surface drainage patterns, whether it was sheltered or unsheltered from the sun (by trees, shrubs or rocks), and, if sheltered, its compass orientation (in 4 quadrants) with respect to the sheltering object. Seedling distribution with regard to sheltering objects was analyzed with a Chi-square test. In 3 of the 15 quadrats seedlings were simply counted, since the canopy was essentially closed, i.e., all seedlings in these quadrats were sheltered from the sun.

RESULTS

The general physical characteristics of the 15 quadrats are presented in Table 1. The communities ranged from dominant ponderosa pine (*Pinus ponderosa*) to mixed conifer communities. Gambel oak was usually a relatively minor component. More complete descriptions of these communities may be found in Layser and Schubert (1979).

The three contiguous quadrat sites on Humphrey Peak (Table 1) were of low-density ponderosa pine averaging 43 ± 35 pines/ha with an average dbh of ca. 40 cm. Gambel oak density on each quadrat was ca 20 genets/ha with 1–2 stems per clone and an average dbh of 17 cm/stem. These quadrats represent a gradient from a swale to a neighboring ridge. This is most evident by a combined increase in *Cowania* sp. and *Cercocarpus* sp. from zero in quadrat 1 to 8 in quadrat 2 and more than 100 in quadrat 3. Gambel oak seedling density was relatively high (range 360–590) and without apparent pattern along this steep environmental gradient.

Quadrats 4–9 were located on the flat Mogollon Rim south of Flagstaff in mature ponderosa pine forest averaging 350 ± 112 stems/ha with an average dbh (in each quadrat) ranging from 31 to 46 cm. Mature oak density was low in these quadrats, averaging ca 10 genets/ha with 1–7 stems per clone and an average dbh of ca 16 cm per stem. Seedling density in these six quadrats ranged from 240 to 860 ha. Quadrat 9, which had the highest seedling density (860/ha) of this group, was flanked by five large oaks.

Quadrats 10–12 represent three distinct habitats in the Pinedale area of the Mogollon Rim, a south-facing slope (No. 12), a relatively

TABLE 1. Site characteristics for the 15 quadrats (redundant data are not repeated within a geographic region).

Quadrat number	Geographic region	Latitude (decimal)	Longitude (decimal)	Elevation (meters)	Slope	Aspect	Soil WHC[1]	Canopy species[2]
1	Humphrey Peak	35.27	111.6	2226	17°	S 80° E	32-88/45-60	PIPO/QUGA
2					25°	N 70° E		PIPO/QUGA
3					25°	N 75° E		PIPO/QUGA
4,5,6	Flagstaff	35.03	111.73	2165	0°		40-90/50-77	PIPO/QUGA
7,8,9		35.00	111.67		8°	N 65° E	40-90/50-77	PIPO/QUGA
10	Pinedale	34.3	110.25	1982	4°	N 45° W	unknown	PIPO/QUGA
11				2012	0°			PIPO/QUGA/ JUXX
12				1982	20°	S 10° E		PIPO/QUGA/ JUXX
13	Sandia Mountains	35.13	106.53	2226	15°	S 80° E	46-122/58-65	PIPO/PIED/ JUXX/QUGA
14					10°	S 60° E	40-85/42-46	PIPO/PIED/ JUXX/QUGA
15		35.15	106.53	2165	23°	S 30° W	54-66/60-62	PIPO/PIED/ JUXX/QUGA

[1] WHC = Water Holding Capacity (%). A range of water holding capacities is reported for the soil surface layer and at a depth of 30 cm (Neilson and Wullstein 1983).

[2] PIPO = *Pinus ponderosa*, QUGA = *Quercus gambelii*, PIED = *Pinus edulis*, JUXX = *Juniperus* sp.

flat lowland area (No. 10), and a flat plateau area. All three areas possessed a high density of seedlings, with the plateau exhibiting the greatest number (1,080/ha). All three areas had been artificially thinned, but still possessed a fairly dense canopy. Quadrats 10 and 12 were primarily mature ponderosa pine with ca 500 stems/ha and an average dbh of 18 and 27 cm, respectively. Quadrat 11 was mixed conifer/oak woodland.

Quadrats 13–15 in the Sandia Mountains, New Mexico, were characterized by mixed conifer forest with a Gambel oak component. Quadrat 15, on a south-facing slope, was similar in seedling density to most other quadrats, with 513 seedlings/ha. Quadrats 13 and 14 were on east-facing ridges. These quadrats were of the same elevation and aspect and were within 1 km of each other. Quadrat 14 was located on a primary ridge separating major drainage basins. It was at a lower angle than No. 13 and contained more bare ground. Quadrat 13, by contrast, was located on a ridge within a major drainage basin, was at a steeper angle, and contained less bare ground than No. 14. By virtue of their close proximity, the two quadrats would be expected to receive similar amounts of rainfall. Because of its position as a drainage divide, the primary input of moisture to Quadrat 14 was likely limited to incident rainfall. Quadrat 13, however, received moisture from both rainfall and runoff from the surrounding basin within which it occurred. This was particularly evident from extensive rill development, which was absent on Quadrat 14. Quadrat 13 possessed 1,320 seedlings/ha in contrast to 120 seedlings/ha in Quadrat 14.

Table 2 indicates the number of seedlings in sheltered and unsheltered positions for each of the quadrats. Quadrats 11, 13, and 15 were too dense to allow judgements of sheltering. Sixty percent (341/571) of the seedlings in 12 quadrats (i.e., excluding quadrats 11, 13, and 15) were scored for their orientation with regard to a sheltering object (Table 2, Fig. 1). The distribution is significantly skewed ($X^2 = 33.74$, $P \ll .01$) to the NE quadrant.

Age estimates of 14 randomly collected seedlings (<30 cm crown height) ranged from 6 to 17 years. Regressions of root length against root diameter indicated root taper ranging from $-.06$ to $-.19$ mm/cm (r^2 ranged from .81 to .99). Since these measurements were obtained from broken taproots, total root length was extrapolated from the regression equations and found to range from 40 to 114 cm. Root growth rates were estimated to range from 2.7 to 11.4 cm/yr.

DISCUSSION

Several points are apparent from these data. First, Gambel oak seedlings are abundant and widely distributed in the southern part of the range of this species and are rare in

TABLE 2. Total seedlings (sheltered and unsheltered) per quadrat.

Quadrat no.	Sheltered	Unsheltered	Seedlings/ hectare
1	40	19	590
2	16	20	360
3	32	16	480
4	24	20	440
5	29	6	350
6	14	10	240
7	19	20	390
8	12	13	250
9	58	28	860
10	50	37	870
11	unknown	unknown	1080
12	35	41	760
13	unknown	unknown	1320
14	12	0	120
15	unknown	unknown	513

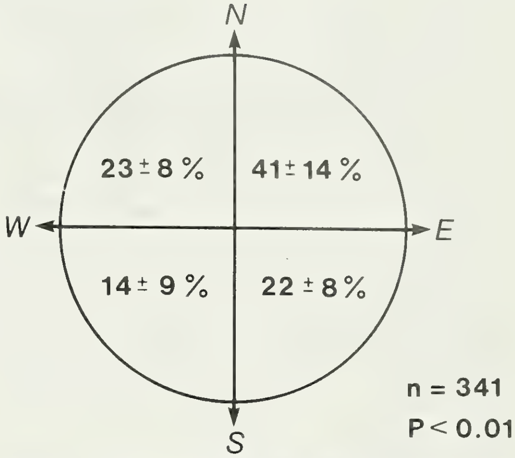

Fig. 1. Compass orientation of seedlings (% per quadrant) associated with a sheltering object in all quadrats, excluding quadrats 11, 13, and 15 (see text for explanation).

the northern part of the range. Second, mature Gambel oak is a relatively minor component of the ponderosa pine–mixed conifer forest. Third, although Gambel oak does clone in Arizona and New Mexico, the apparent number of ramets per clone is relatively few (1–7 in the quadrats sampled, although larger numbers can be found) compared to the hundreds to thousands of ramets per clone that are common in the northern parts of the range (Brown 1958, Ream 1963). A corollary to this point is that mature ramets are much larger in the south than in the north, where dbh is typically in the range of 5–8 cm (Brown 1958, Ream 1963) compared to 16–17 cm in the south. Fourth, although seedlings are widespread across a range of microhabitats, their distribution and abundance does appear to reflect some dependence on soil moisture.

This last point is most interesting. We previously reported (Neilson and Wullstein 1983) that seedling survival in the southern parts of the range was largely independent of microhabitat, being high in all situations from sheltered to unsheltered. The three contiguous quadrats on Humphrey Peak are in support of this contention. Whereas the shrub distribution indicated considerable edaphic and/or hydrologic differences between the swale and ridge habitats, the seedling density across this gradient indicated no trend. Nevertheless, 60% of the seedlings in these and the other quadrats did exhibit a strong pattern of sheltering, apparently favoring mesic microhabitats. This is further supported by the two ridge quadrats in the Sandia Mountains. One ridge was apparently swept frequently by surface flow, as indicated by the extensive rill development and the location of the ridge within a major drainage basin. Intense summer thunder showers are common in this region (Bryson and Lowry 1955). This ridge contained the highest density of seedlings observed in any of the quadrats, notwithstanding the apparently high surface wash. A neighboring ridge, a major drainage divide, apparently received little to no runoff from the surrounding landscape, as indicated by the absence of rills. This ridge contained the lowest density of oak seedlings observed (all of which were sheltered) in any of the quadrats. In almost every respect but hydrology, the two ridges appear to be similar. This suggests that even in a region where summer rain is relatively high, a consistently mesic microhabitat may be required to provide adequate soil moisture for seedling survival.

The six quadrats on the relatively flat Mogollon Rim south of Flagstaff present some evidence that the density of seedlings is not entirely independent of the density of adults. Five of these quadrats possessed seedling densities ranging from 250 to 440 per hectare (quadrats 4–8), whereas one (quadrat 9) possessed a seedling density of 860 per hectare (Table 2). All these quadrats contained a similar density of mature oaks. However, quadrat 9 with the highest seedling density in this region, was flanked by five large oaks, suggesting some dependency of seedling density on the local density of seed–bearing trees.

Since seedling density was found to be relatively high throughout the oak zone in the southwest, why are mature oaks relatively rare in these forests? It may be that conifer seedlings, which are also abundant in these forests, grow much more rapidly than the oaks and gain dominance through competition for light and moisture. Several oak seedlings (of less than 30 cm stature) were aged on the basis of taproot rings and were judged to be from 6 to 17 years old. By contrast, ponderosa pine raised in several provenance gardens in the Great Plains grew between 0.7 and 3.9 m in 10 years (Read 1983). Thus, overtopping of oak seedlings by ponderosa pine seedlings may competitively inhibit the growth of oaks.

Once past the establishment phase, the position of oaks in the landscape is apparently independent of minor differences between microhabitats. The density of mature oaks was relatively uniform between all the quadrats, which varied considerably in topography. The ultimate fate of seedlings, once established (i.e., taproot developed), is likely determined by biotic factors, including competition with pines and herbivory from insects and vertebrates (primarily rabbits and cows) (Neilson and Wullstein 1983).

In conclusion, where Gambel oak is least abundant in its geographic range, it is capable of sexual reproduction, seed dispersal, and seedling establishment. Conversely, where Gambel oak is most abundant in its geographic range, near the northern limits, its mode of reproduction is primarily asexual. The establishment of Gambel oak seedlings is dependent on consistent soil moisture, even in areas where summer rainfall is high. These results support the hypothesis that Gambel oak in northern Utah, existing today by asexual reproduction, was likely established as a relatively minor component of a mixed pine/oak woodland under a mid-Holocene climate with more favorable summer moisture conditions in northern Utah than presently occur (Cottam, Tucker, and Drobnick 1959, Neilson and Wullstein 1983).

ACKNOWLEDGMENT

We thank R. Seiler for valuable assistance in data collection. This work was supported by the Department of Biology, University of Utah.

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FEEDING HABITS OF METAMORPHOSED *AMBYSTOMA TIGRINUM MELANOSTICTUM* IN PONDS OF HIGH pH (> 9)

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ABSTRACT.—During the spring breeding season throughout the channeled scablands of eastern Washington, metamorphosed male and female blotched tiger salamanders (*Ambystoma tigrinum melanostictum*) utilize oropharyngeal suction to capture large quantities of small aquatic invertebrates. Stomach content analysis on salamanders from three populations of this subspecies revealed that they consume the following taxa: Copepoda, Cladocera, Culicidae, Anostraca, and Chironomidae. Although the amount of energy obtained by adults via in-water feeding was not calculated, the large volume of aquatic invertebrate material flushed from salamander stomachs suggests that this feeding strategy should add significantly to their total annual nutrient consumption.

Investigations on the feeding habits of *Ambystoma tigrinum* have centered primarily on the diets of branchiate individuals. This ontogenetic stage, depending on individual size, season, and locality, feeds daily on large quantities of a variety of prey items (Olenick and Gee 1981, Brophy 1980, Dodson and Dodson 1971). As a result of their secretive terrestrial habits (Nussbaum et al. 1983, Smith 1961, Sever and Dineen 1978) similar information on diet and feeding for transformed individuals has been difficult to obtain. Reports on the feeding habits of this developmental stage are largely restricted to general accounts that list a variety of terrestrial invertebrates (most often those accepted by captive salamanders) as potential prey (Conant 1975, Nussbaum et al. 1983, Johnson 1977, Smith 1961). Since some metamorphosed *A. t. melanostictum* in central and eastern Washington remain in the ponds for considerable period of time as adults during the breeding season or as subadults immediately following transformation, such individuals could utilize the abundant aquatic invertebrate communities as an energy source.

In numerous locations larval *A. t. mavortium* metamorphose during late summer or early fall and remain in the ponds throughout the winter (Webb and Roueche 1971). The extent to which these transformed individuals feed during this period is unknown, but Webb and Roueche (1971) found aquatic prey in the stomachs of 13 subadults collected in the stomachs of 13 subadults collected in Dona Ana County, New Mexico, in February, and Burger (1950) reported that the principal item in the stomachs of adult *A. t. nebulosum* was the pond snail, *Lymnaea stagnalis*. Sexually mature, metamorphosed tiger salamanders return to the ponds to breed. Egg deposition typically occurs during late winter or early spring (Semlitsch 1983, Hassinger et al. 1970, Bishop 1943, Sever and Dineen 1978), whereas migrations to the ponds occur during spring and/or autumn (Semlitsch 1983, Stine 1984, Smith 1961). Even though transformed *A. tigrinum* may spend several months in the water, they reportedly feed very little if at all (Rose and Armentrout 1976, Stine 1984). However, we found the stomachs of transformed male and female *A. t. melanostictum*, collected from ponds in Washington State during the spring breeding season, often filled with aquatic invertebrates. The following reports on in-pond feeding by breeding congregations of transformed *A. t. melanostictum* and its possible significance.

MATERIALS AND METHODS

Transformed tiger salamanders were seined from three fish-free ponds in the channeled scablands of central and eastern Washington (14 April to 6 May 1984). This region is a network of scoured canyons and deep valleys carved out of basalt bedrock and loess by the Spokane flood of 20,000 years ago (Bretz

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1959). Thin soils characterize the scablands, and the dominant vegetation is a sagebrush (*Artemesia*)-wheatgrass (*Agropyron*) association (Daubenmire 1970). Nineteen salamanders were collected from a saline (300 $\mathrm{mOs_m}$), alkaline (10.1 pH) pond in southern Grant County, 11 km from an alkaline (10.1 pH) pond of low salinity (<5 $\mathrm{mOs_m}$) in southern Lincoln County, and 9 km from an ephemeral pond in northernWhitman County. Following capture the specimens were immediately immersed in an ice solution and returned to the laboratory, where they were either anesthetized in 1:1000 MS222 or frozen to −80 C. Stomach contents were obtained from either the anesthetized individuals using a flushing method modified after that of Legler and Sullivan (1979) or from the excised stomachs of the frozen animals. All stomach contents were stored in 70% ETOH until identified.

Table 1. Summary of stomach content analyses for metamorphosed *A. t. melanostictum* from eastern and central Washington ponds.

	Percentage of stomachs containing taxon/ percentage of total items consumed / average number per stomach containing taxon		
	Lincoln Co. N = 11	Whitman Co. N = 9	Grant Co. N = 16
Copepoda	91/55/78	100/75/102	6/10/164
Cladocera	73/26/47	—	—
Anostraca	—	89/21/32	—
Ostracoda	73/04/06	67/02/03	—
Culicidae	9/ */01	—	100/45/044
Chironomidae	9/ */01	—	94/41/043
Trichoptera	73/06/11	33/01/04	—
Notonectidae	27/ */01	22/ */01	31/01/002
Corixidae	—	11/ */01	38/ */001
Odonata	9/ */01	—	13/ */001
Dytiscidae	82/03/05	78/02/04	19/02/009
Curculionidae	36/ */01	—	—
Gastropoda	45/05/14	—	—
Acarina	—	—	6/ */001

* $< 0.5\%$

Results and Discussion

Thirty-six (92%) of the 39 transformed *A. t. melanostictum* examined contained aquatic invertebrates in their stomachs; material in the remaining three individuals could not be identified. No apparent differences in the percentage of stomachs containing food were detected between males and females from any of the three populations. The structure of the aquatic invertebrate communities varies from pond to pond, and therefore the differences in the diets of these salamander populations reflect this factor.

The kinds of prey utilized by this subspecies in eastern Washington ponds are similar to those reported for various larval conspecifics (Brophy 1980, Dodson and Dodson 1981, Dineen 1955) and related larval congenerics (Branch and Altig, 1981). Although the total number of food items per stomach varied from 7 to 431 ($\bar{x} = 118$), the most common prey eaten by salamanders inhabiting the ponds included: Copepoda and Cladocera (Lincoln County); Copepoda, Cladocera, and Anostroca (Whitman County); and Chironomidae and Culicidae (Grant County) (Table 1). Although not quantified, these invertebrates also composed the largest stomach content volume in the majority of water-collected salamanders. Therefore, small aquatic invertebrate taxa are responsible for the bulk of the diet of transformed adult *A. t. melanostictum* from the ponds investigated.

It is clear from our observations on metamorphosed *A. t. melanostictum* maintained in aquaria and supplied quantities of aquatic invertebrates that prey capture is accomplished by oropharyngeal suction, a nearly universal method of those vertebrates feeding in water (Bramble and Wake 1985). The large number of prey items present in the stomachs of both male and female transformed salamanders indicates that they feed extensively while in the ponds during the breeding season. This observation differs from that of Rose and Armentrout (1976); they rarely found food in the stomachs of metamorphosed *A. t. mavortium* collected from ponds. Smallwood (1928) determined that adult *A. maculatum* stop eating when they become aquatic during the breeding season, and Anderson (1968) reported that transformed male, but not female *A. macrodactylum* feed in the ponds.

The amount of time that *A. t. melanostictum* spends in water during the year is unknown. Therefore, the importance of energy obtained from in-water prey capture has not been determined. However, such feeding probably adds significantly to the total yearly energy intake, particularly within the channeled scablands of Washington where terrestrial conditions are harsh and land-living prey may be less readily available.

Metamorphosed *A. t. melanostictum* apparently spends long periods of time each year in these high pH ponds that readily support exploitable, abundant aquatic invertebrate communities and contain few predatory fish (Tillett 1984). This strategy is probably adaptive, since the terrain adjacent to these scabland ponds is, at best, marginal salamander habitat.

ACKNOWLEDGMENTS

The authors are grateful to R. E. Herrington and E. Johnson for their assistance in the field.

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NOTES ON THE SWAINSON'S HAWK IN CENTRAL UTAH: INSECTIVORY, PREMIGRATORY AGGREGATIONS, AND KLEPTOPARASITISM

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ABSTRACT.—A premigratory flock of Swainson's Hawks numbering at least 213 individuals was observed during July and August of 1984. Aerial feeding on grasshoppers was noted and kleptoparasitism was recorded between the Swainson's Hawk and the American Kestrel.

Swainson's Hawk (*Buteo swainsoni*) inhabits open spaces such as plains, prairies, and deserts. Prior to the turn of the century this species was an abundant resident of several western states (Bent 1937). A specimen was collected in Utah's Wasatch Mountains as early as 1868, and the species was reported as a common nesting resident of Summit County, Utah, in 1877 (Hayward et al. 1976).

Yet, Swainson's Hawk could not be considered abundant in central Utah today. For instance, during a 12-month Great Basin raptor survey 1,275 individual raptors representing 12 species were sighted, yielding an average of one sighting per every 10 km traveled. By comparison, nearly 400 km were traversed between each Swainson's Hawk sighting (Woffinden and Murphy 1977a). Furthermore, only one nesting pair has been reported for Cedar Valley, Utah County, Utah (40°00′N, 111°55′–112°35′W) during the past decade (Woffinden and Mosher 1979).

Cedar Valley, situated near the eastern limit of the Great Basin, is characterized by typical cold desert vegetative associations (Shelford 1963). Two small villages, Cedar Fort and Fairfield, are located in the extensively cultivated northern portion of the valley. Except for numerous black willows (*Salix nigra*) associated with these communities, the valley is devoid of large trees. The area supports a sizable raptor community and has been the site of a number of recent studies (Murphy et al. 1969, Smith and Murphy 1973, Woffinden and Murphy 1977b).

On 23 July 1984, 36 Swainson's Hawks were observed immediately west of Fairfield. Subsequently, 213 individuals were counted during a visit to the area on 6 August, and 59 were observed on 16 August 1984. All the birds were dark or rufous phase individuals (Brown and Amadon 1968:585), and many had lost flight and/or tail feathers. This unusual accumulation represents the largest flock of Swainson's Hawks ever reported for this portion of the state.

Although the aggregation was apparently a premigratory gathering, it was impossible to determine accurate arrival and departure dates.

However, a local resident stated that large numbers of hawks first appeared near the middle of July. Large flights of Swainson's Hawks have been reported for several areas throughout the United States (Bent 1937, Cruickshank 1937, Fox 1956, Martin and McEneaney 1984), but premigratory accumulations of the magnitude reported here have rarely been recorded.

Swainson's Hawk is noted for its insectivorous diet (Bent 1937, Taylor 1946, Hayward et al. 1976). For instance, White (1966) recovered 230 crickets from a female collected on a Kansas farm. However, the species consumes a variety of other organisms, including mammals, birds, reptiles, amphibians, fish, crayfish, and beetles (Bent 1937, White 1966, Sexton and Marion 1974, Dunkle 1977, Bechard 1983). In spite of the early reports of insectivory, recent studies suggest that mammals make up the major portion of the hawk's diet (Dunkle 1977, Fitzner 1977, Bechard 1980, 1983).

Twenty Swainson's Hawks were observed soaring near Fairfield, Utah, on the afternoon of 23 July 1984. An additional 16 individuals were perched in a group of nearby trees. Swarms of grasshoppers (*Melanoplus femurrubrum*) were observed in the area flying from the ground or vegetation and ascending to considerable heights.

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Soaring hawks were observed repeatedly extending one or both feet to quickly snatch ascending grasshoppers. All but four of the perched birds joined the soaring flock during the 15 minutes they were observed actively feeding. By 1745 h the hawks had drifted out of sight to the west, and only a few airborne grasshoppers were still visible. This unique feeding behavior corresponds exactly with an account in Bent (1937:229). Similar Swainson's Hawk feeding behavior was noted during one other visit to the area.

Although the hawks were taking advantage of an abundant food source, it is not known if the grasshopper outbreak was responsible for the unusual aggregation noted. Grasshoppers were also abundant during the summer of 1972, but large groups of Swainson's Hawks were not observed in the area at that time. The bulk of the hawks were confined to the Fairfield locale; only four were sighted during searches throughout much of the remainder of the valley.

Kleptoparasitism (interspecific food stealing or piracy) has been reported for several avian families (see Brockman and Barnard 1979 for a review). Heredia and Clark (1984) summarized the occurrence of this behavior among the raptors, including four buteonine species as participants. Swainson's Hawk was excluded. Piracy involving this species and the American Kestrel (*Falco sparverius*) is reported here.

Approximately 34 Swainson's Hawks and 3 Kestrels were observed in the immediate vicinity of Fairfield on 16 August 1984. Several of the buteos were soaring; the remainder were perched in trees, on fence posts, and on utility poles. A Kestrel holding an unknown species of small mammal was perched on a utility line some distance from Swainson's Hawks. It flushed as the vehicle approached and flew a few meters before alighting again on one of the conductors. The procedure was repeated several times. Each flight brought the Kestrel nearer to the perched hawks.

Finally, two Swainson's Hawks left their perch in a nearby tree and flew directly at the Kestrel. After flushing the Kestrel from the line, they actively pursued it for several seconds. In response to the harassment, the Kestrel dropped the prey it was holding. One of the pursuing hawks caught the falling prey before it reached the ground, only to be vigorously chased by the second. The prey was dropped once more and fell to the ground. Both hawks made a few cursory passes over the site and then flew to nearby fence posts where they remained perched during the duration of my visit. The Kestrel returned to the utility line.

Brockman and Barnard (1979) suggest that continual raptor interactions at feeding areas may promote piracy. The deliberate actions of the Swainson's Hawk I observed suggest previous piratical experience. Since the site is prime Kestrel habitat and the Swainson's Hawks had been residents of the area for several weeks, the possibility of previous interspecific interactions was likely. Heredia and Clark (1984) suggest that similar niche overlap may have played a role in the piracy they observed between the Black-shouldered Kite (*Elanus caeruleus leucurus*) and White-tailed Hawk (*Buteo albicaudatus*). Although kleptoparasitism is a frequently observed avian behavior, it appears to occur opportunistically and is probably not an important feeding strategy (Fuchs 1977, Maxson and Bernstein 1982).

I thank Gary B. Jolley for field assistance. D. M. McNair and M. Bechard commented on an earlier draft. Financial support was provided by the University of Pittsburgh at Johnstown.

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TURKEY VULTURES DECLINE AT A TRADITIONAL ROOSTING SITE

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ABSTRACT.—A population decline of about 50% from 1974 to 1981 for Turkey Vultures (*Cathartes aura*) was found at a traditional roosting site at Malheur National Wildlife Refuge in Oregon. This decline may have been due to a region-wide reduction in this species, to the possible but improbable formation of a new but undiscovered roost, or to a reduction in feeding opportunities caused by the decreased use of the refuge by cattle.

Concern has been expressed in some regions of the United States over population declines of Turkey Vultures (*Cathartes aura*), resulting in the placement of this species on the National Audubon Society's Blue List twice since 1972 (Tate 1981). Vulture populations appear to be increasing in parts of the east and decreasing in some areas of the west (Tate and Tate 1982), but more quantitative data are needed.

Brown (1976) analyzed winter population trends for Turkey and Black Vultures (*Coragyps atratus*) from Christmas Bird Count data from 1950 to 1973 for 16 eastern states, Arizona, Texas, California, and the District of Columbia. He found that Turkey Vultures had declined steadily over this 24-year period in all of these states except California. He attributed the exception of California to large vulture populations from areas censused only in recent years.

Since at least 1935, Turkey Vultures have traditionally roosted at the P Ranch Station at the south end of Malheur National Wildlife Refuge, Harney County, Oregon (Davis 1974). The vultures roost in a row of tall cottonwoods (*Populus* sp.) but use a metal observation tower for pre- and postroosting. They can be accurately censused in both places.

In 1973 Davis (1974) censused the vultures at P Ranch from late spring to late summer and found a mean of 104 birds per night (range 68–151: N = 28). There was some seasonal variation, with more birds in the spring and late summer. Her census periods from 21 May to 20 June and 21 June to 20 July had high counts of 106 and 110, respectively. There was a mean of 90 birds from seven counts during these periods.

At P ranch I made 16 censuses of Turkey Vultures in 1981 from 23 May to 2 July and 22 counts in 1982 from 25 May to 7 July. In 1981 I counted only the peak number of birds on the tower, but the next year I also counted additional birds in the cottonwoods. The mean in 1981 was 46.6 birds (range 35–54), and the following year it was 54.0 (range 33–74) altogether, with 49.6 birds (range 33–69) on just the tower. The means of these two years is little more than half that of 1973, and there is almost no overlap between the ranges of the 1973 counts and those of 1981 and 1982.

The only count between 1973 and 1981 that I am aware of was one of 92 vultures on 1 July 1976, indicating populations were still comparatively high that year.

There are at least three possible reasons for this population decrease. One is that there has been an overall decrease of vultures in the region. This would support Brown's earlier findings (1976). Another possibility is the establishment of new roost sites, but no new large roost sites are known in the area, which receives considerable attention from amateur bird watchers. A third explanation for this population decrease is that it is a local decline caused by the cutting back in the number of cattle on the refuge, with a shift to greater winter use. In 1972-73 Animal Unit Months (AUMs) on the refuge were 126,593 (Malheur National Wildlife Refuge, unpublished report). This has decreased to 45,000 AUMs in 1981 and 46,000 AUMs in 1982. Since vultures are known to scavenge dead cattle (Bent 1937, Burleigh 1972), the reduction of this potential food source might be responsible for the vulture decline.

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Whatever the reason, this summer population of vultures has evidently suffered a large decrease since 1973. Because this species may be in trouble in general, and many roosts can easily be censused, efforts should be made to do so over the entire range of the vulture to determine population trends.

I thank the personnel of Malheur National Wildlife Refuge for providing housing and support while this study was conducted. The study was funded in part by the nongame program of the Oregon Department of Fish and Wildlife.

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BARN OWL DIET INCLUDES MAMMAL SPECIES NEW TO THE ISLAND FAUNA OF THE GREAT SALT LAKE

Carl D. Marti[1]

ABSTRACT.—An investigation of the diet of the Common Barn-owl (*Tyto alba*) on Antelope Island, Great Salt Lake, Utah, yielded four mammal species not previously known to occur on any island in the Great Salt Lake (*Microtus pennsylvanicus*, *M. montanus*, *Ondatra zibethicus*, and a *Sorex* sp.). Two other species, known from other islands, were added to the list of fauna of Antelope Island (*Perognathus parvus* and *Reithrodontomys megalotis*). The barn owl diet on Antelope Island was remarkably like that of barn owls feeding in farmlands adjacent to the Great Salt Lake despite major vegetational differences.

Relatively little collecting for small mammals has occurred on islands in the Great Salt Lake, Utah; the remoteness of several islands and private ownership of others have discouraged a thorough examination of their mammalian fauna. Bowers (1983) compiled a list of nonvolant, native mammal species known to occur on these islands from previously published studies.

In this paper I document the occurrence of four mammal species previously unreported on any island in the Great Salt Lake and add two additional species to the list for Antelope Island. These mammals were identified among prey remains in pellets of the Common Barn-owl (*Tyto alba*) nesting on Antelope Island. Barn owls have taken certain small mammals in several other localities before mammalogists were aware of the existence of the mammals there (e.g., Stickel and Stickel 1948, Twente and Baker 1951). I also compare the island diet with prey eaten by barn owls feeding in farmlands adjacent to the Great Salt Lake.

METHODS

Regurgitated pellets were collected from a barn owl nest site at the Dooley Ranch on the east-central shore of Antelope Island, Davis County, Utah. The nest was in an abandoned agricultural silo. Pellets were gathered once or twice a year in spring or summer from 1980 through 1984. I documented nesting at the collection site from 1981 through 1984 and believe that nesting probably occurred in 1980 as well. Thus, the material consisted of prey of pairs of owls and their young.

I treated pellets with a sodium hydroxide solution to dissolve hair and feathers. Bones were identified and quantified by standard procedures (Marti 1974).

RESULTS AND DISCUSSION

The barn owl diet on Antelope Island was typical of the foods of this species elsewhere (Wallace 1948, Glue 1967, Marti 1974), being heavily dominated by mammalian prey (98.4%, Table 1). Three rodents in the diet, meadow vole (*Microtus pennsylvanicus*), montane vole (*M. montanus*), and muskrat (*Ondatra zibethicus*), had not previously been known to occur on any island in the Great Salt Lake, nor had shrews (*Sorex* sp.). The shrews were most likely *S. vagrans*, which occurs on the adjacent lake shore (Durrant 1952). The Great Basin pocket mouse (*Perognathus parvus*) and the western harvest mouse (*Reithrodontomys megalotis*), which also occurred in the owl diet, had not been reported previously for Antelope Island but were known from other islands in the Great Salt Lake (Bowers 1983).

Even though little is known about small mammal populations on these islands, several apparent anomalies existed between the owl diet and probable prey abundance and distribution. The heavy domination by voles was the most surprising aspect of the barn owl

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TABLE 1. Prey of Common Barn-Owls on Antelope Island, Great Salt Lake, Utah.

	Percent of prey numbers					Totals	
Prey	1980	1981	1982	1983	1984	No.	Percent
Sorex sp.	2.0	2.3	3.6	2.8	3.6	73	2.7
Sylvilagus nuttallii (juv.)	0.1	—	—	—	—	1	tr.
Perognathus parvus	0.5	—	—	—	—	6	0.2
Dipodomys ordii	0.2	—	—	—	0.3	5	0.2
Reithrodontomys megalotis	9.5	19.2	11.9	3.3	5.9	246	9.0
Peromyscus maniculatus	5.0	4.3	1.1	2.5	6.6	124	4.5
Neotoma lepida	0.1	—	—	—	—	1	tr.
Microtus pennsylvanicus	55.6	49.8	62.8	70.7	61.7	1617	59.2
Microtus montanus	25.3	20.8	16.6	16.8	19.7	590	21.6
Ondatra zibethicus (juv.)	0.2	—	—	—	—	2	0.1
Mus musculus	0.5	2.7	1.4	0.2	0.5	21	0.8
Birds							
Porzana carolina	—	0.4	—	—	—	1	tr.
Sturnus vulgaris	—	—	—	0.5	0.3	4	0.1
Unidentified bird	0.8	0.4	2.5	3.0	0.7	34	1.2
Insects							
Unidentified coleopteran	0.2	—	—	—	0.5	5	0.2
Totals	1231	255	277	393	574	2730	100.0

*tr = <0.01%

diet. Habitat suitable for voles was very limited on Antelope Island; dense vegetation usually associated with them occurred only in a narrow band at a few places along the lake shore, around a few springs, and in an irrigated hay field. The owls must have concentrated their foraging efforts in those limited areas. The deer mouse (*Peromyscus maniculatus*) is the most abundant small mammal on the islands in the Great Salt Lake (Neil Jensen, personal communication), but they ranked only a distant fourth in species abundance in the owl diet. The valley pocket gopher (*Thomomys bottae*) was the only small nocturnal mammal known to exist on the island not taken by the owls.

My continuing, long-term study of barn owl ecology in Box Elder, Weber, and Davis counties, Utah (Marti unpublished data) overlapped with the years reported here for the Antelope Island material. Data from the long-term study, being done in agricultural land, provides some interesting comparisons for the Antelope Island data. Antelope Island and the main study area are 27 km apart at the closest point. Major differences between the two sites are in vegetation and topography. The mainland study area is essentially flat, and irrigated crops and pastures replace native vegetation. Antelope Island has much more topographic relief, rising from about 1,260 m to 1,999 m, and is covered almost entirely with vegetation typical of Great Basin deserts. Despite these differences, the same five prey genera (*Microtus*, *Peromyscus*, *Reithrodontomys*, *Mus*, and *Sorex*) contributed 97% of the diet in both areas. Only minor differences in the order of species abundance occurred between diets in the two areas. Meadow voles and montane voles were first and second in both, whereas deer mice and harvest mice exchanged places (third and fourth), as did house mice (*Mus musculus*) and shrews (fifth and sixth) between island and mainland. Year-by-year comparisons between island and mainland diets showed that shrews and house mice were taken less frequently in every year on the island than on the mainland. Deer mice occurred less frequently in the island diet for four of five years, but the reverse was true for harvest mice. The two vole species combined were more frequent prey on the island in three of five years and overall (80.8% versus 77.5%); meadow voles were taken at a higher frequency in every year of the island than on the mainland, but the opposite was true for montane voles. The desert woodrat (*Neotoma lepida*) and Ord's kangaroo rat (*Dipodomys ordii*) were in the island but not the mainland diet. Habitat for these has been eliminated by irrigation agriculture in the mainland study area. Two other species, the Norway rat (*Rattus norvegicus*) and pocket gophers, were eaten by owls on the mainland but not on the island. Norway rats probably do not occur on the island, which has had very little human habitation, but pocket gophers are found there. I cannot offer a satisfactory explanation of why island barn owls did not appear to capture gophers.

It is presumed that the Antelope Island barn owls foraged entirely on the island and, thus, that their diet reflected prey species found there. I base this on investigations of barn owl foraging ranges done elsewhere and on the tenets of central-place foraging theory. Orians and Pearson (1979) contended that animals should reduce costs of obtaining food as much as possible. One way to do this is to forage close to the nest site (central place) and reduce traveling time. For the Antelope Island barn owls this means foraging on the island and not crossing over to the mainland to hunt. Minimum distance from the island collection site (nest/roost) to the mainland was more than 10 km during 1980–1984. Hegdal and Blaskiewicz (1984) found a maximum distance from roost to hunting areas of 5.6 km in radio-tagged barn owls.

Note that these comparisons are between the diet from one collection site each year on the island and 26–31 sites on the mainland. The sample size from the mainland was much larger (n = 41,453) and represented year-round prey data whereas the island sample was mainly from late winter through summer. Although these differences could affect comparisons between diets from the two sites, it seems unlikely that they would cause major misconceptions.

In conclusion, barn owls selected very similar prey on Antelope Island and in agricultural lands adjacent to the Great Salt Lake despite the very different vegetation in the two places. Dietary evidence indicated that the owls concentrated their foraging efforts in habitat suitable to voles in both localities. This type of habitat is abundant and widespread in the mainland study area but limited and concentrated on Antelope Island.

ACKNOWLEDGMENTS

I thank the following employees of the Utah Division of Wildlife Resources for help in gaining access to Antelope Island and in collecting pellets: Phillip Wagner, Don Paul, and John Kimball.

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DISTRIBUTIONAL STUDY OF THE ZION SNAIL, *PHYSA ZIONIS*, ZION NATIONAL PARK, UTAH

David Ng[1,2] and James R. Barnes[1]

Abstract.—The major hanging gardens and associated water seeps in Zion National Park were surveyed for the presence of the Zion Snail (*Physa zionis*). Environmental parameters, including water depth, water velocity, substrate slope, and algal cover, were measured to determine their effect on the local distribution of the snail. Large populations (densities 125 to 250/m^2) were found in the Virgin River Narrows area of the park and at a hanging garden and seep located 1.0 km north of Scout Lookout. Densities in other localities were low in comparison. Snails were not found in all hanging gardens or seeps. The major factor controlling within seep distribution was determined to be water velocity. Experiments were conducted to test the ability of the snail to remain attached during differing water flows. The snail showed an ability to remain attached during high flows, but few snails were found in areas of high flow.

The Zion Snail, *Physa* (*Petrophsa*) *zionis* Pilsbry (1926), an endemic to Zion National Park, Washington County, Utah, is found in water seeps and associated hanging gardens on the canyon walls along the Virgin River Narrows region of the park. The limpetlike characteristics of *P. zionis*, a reduced shell spire, enlarged last whorl, and large foot, were reported as being adaptations for attachment on vertical surfaces of seeps (Pilsbry 1926, Chamberlain and Jones 1929). There is no literature on the ecology or natural history of the Zion Snail other than the mention of a snail-algae association and the hypothesis that *P. zionis* evolved from a common *Physa* type (Woodbury 1933, Talmadge 1970).

The purposes of this study were: (1) to survey and determine the distribution and population density of the Zion Snail within Zion National Park, (2) to determine the importance of specific habitat variables which may limit snail distribution within seeps, and (3) to test the hypothesis that the limpetlike morphological adaptations provide the snail with greater substrate attachment abilities in the seep environment.

Study Area

Zion National Park, in southwestern Utah, is in an area of sandstone formations cut by the Virgin River and its tributaries. Seeps and hanging gardens that offer suitable habitat for the Zion Snail are found at the junction of the Navajo and Kayenta sandstone layers. Seeps are formed when water percolating through the porous Navajo layer contacts the impervious underlying Kayenta formation and flows laterally to the canyon walls (Welsh and Toft 1981). The Navajo-Kayenta junction is at different elevations along the canyon wall in relation to the Virgin River. In the Main Canyon area of the park, the river has cut the deepest and seeps are farthest removed from the river. In the Narrows the river is near the Navajo-Kayenta junction elevation, and many of the seeps are close to the river. Malanson (1978, and 1980) describes the plant communities for some hanging gardens in the Narrows region.

Seeps in Zion National Park are located in three regions. They are the Narrows, the Gateway to the Narrows, and Main Canyon. The Narrows, including Orderville Canyon, is a narrow box canyon where vertical canyon walls form the channel of the Virgin River. The canyon walls are less than 10 m apart in some areas. Seeps in the Narrows are mainly simple dripline and window-blind types (Welsh and Toft 1981), though a few low alcoves have been carved out by the river. All seeps have varying amounts of calcium carbonate precipitate and algae. A film of water usually less than 1 mm in depth flows over the vertical and horizontal surfaces. Clinging herbaceous plants and mosses are common, indicating the presence of relatively stable or

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TABLE 1. Classes of ecological parameters used to analyze local distributional patterns within seeps.

	Classes of parameters				
Parameters	1	2	3	4	5
Depth (mm)	0–1	2–3	4–10	>10	
Flow (mm)	<1	>1			
Slope (degrees)	0–10	11–45	>45		
Algae (% cover)	0–12.5	12.5–25	25–50	50–75	>75

old seeps (Malanson 1980). New flows without vegetation are also present.

The Gateway to the Narrows region, immediately downstream from the Narrows, is a more open area that receives heavy visitor use. The Gateway is approximately 1.5 km long, with a paved trail along the east canyon wall. Seeps in this section are large and of the window-blind and alcove types (Welsh and Toft 1981). Plant communities are well developed, with many herbaceous and woody plants present. Calcium carbonate precipitation is extensive, with deposits several centimeters in depth common. Seeps in this section are isolated from the Virgin River.

The Main Canyon, which extends downstream from the Gateway, widens considerably. Seeps and gardens are large alcoves, alcove-plunge basins, or terraces (Welsh and Toft 1981). Water flow in these seeps is generally high, with depths of several millimeters measured. Woody plants and pockets of soil are present in most seeps. Most seeps are connected to the Virgin River by small (< 2.0 m wide) streams with rock-gravel-sand substrates.

A terraced seep-spring area approximately 1 km north of Scout Lookout in the Main Canyon was used to study the ecological variables that may limit local distribution and attachment abilities of the snail. This seep is 10 m wide, with two small springs at the south end. The terraces receive surface flow from areas high on the canyon wall, whereas the springs feed into a small stream. The stream flows over a 5 m waterfall, is joined by flow from the terraces, and then flows for approximately 30 m into the Virgin River. Water temperature in the springs is relatively constant (19–21 C), but the terrace water temperature fluctuates with the ambient air temperature. Moss, algae, and herbaceous plants are present. The substrate varies from thick calcium carbonate deposits on the sandstone wall and terraces to the cobble-gravel-sand stream bottom. Water depth and velocity in the stream range from 0 to > 200 mm and 0 to > 1.0 m/sec, respectively.

METHODS

The major seeps in Main Canyon and Gateway to the Narrows were surveyed during the summers of 1981 and 1982. The Narrows was surveyed only in July 1982 because of the limited time it was accessible. The terraced seep-spring north of Scout Lookout in Main Canyon was sampled 24 October 1981 and 2 April, 24 April, 8 June, and 16 July 1982. Detailed quantitative work in the Gateway region was impractical because of heavy visitor use.

A quadrat (10 x 15 cm) was used to estimate population density. Four variables, including water depth, water velocity, substrate slope, and algal cover, were measured in each quadrat. Quadrats were placed every 30 cm apart along random transects across the water course. The number of transects and quadrats required to sample a seep or spring area varied with changes in the amount of flowing water. Water velocity (force of flow) was determined by measuring in millimeters the amount of water forced vertically into a piece of 2 mm diameter plastic tubing. Substrate slope was measured to the nearest 5 degrees. Snail size was measured to the nearest 0.5 mm in situ. Sampling was limited to seeps accessible without climbing equipment.

Statistical analysis of the measured variables was accomplished by using the Chi-square analysis program in MINITAB (Ryan et al. 1981) and the ANOVA program in RUMMAGE (Scott et al. 1982). For analysis, the measurements were divided into classes (Table 1).

To test the attachment ability of the snail, snails were subjected to various flows in a

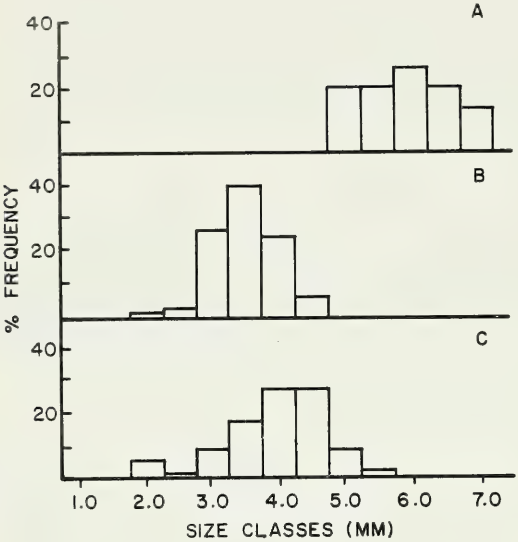

Fig. 1. Size distribution of the Zion Snail found in the Narrows area of Zion National Park. A and B are from seeps in the Main Narrows; C is from Orderville Canyon.

plastic channel and on natural substrate. In the plastic-channel test, snails were placed at the end of a 1 m long plexiglass channel in which water from the stream was channeled through in increasing amounts. In the natural-substrate wash experiment, two volumes of water (5 and 10 liters) were poured down a 15 cm wide plexiglass channel at 5 and 10 second duration onto snails in situ. The channel was held at 30 degrees. For comparison, the more common stream snail, *Physa gyrina*, was tested in the laboratory.

RESULTS

Population Density and Distribution

Our surveys show the Zion Snail occurring from a seep-spring stream area 1 km north of Scout Lookout into Orderville Canyon. The Narrows area above Orderville Canyon was not surveyed in this study. Zion Snails were not found in seeps on the west side of the Virgin River nor south of the seep-spring stream area above Scout Lookout in the Main Canyon area.

NARROWS.—Six seeps examined in this region contained snails. All snails were found in dripline or window-blind type seeps where vegetation was abundant. Many snails were observed less than 10 cm above the Virgin River. Snails were not found on the northwest canyon wall. Of the six seeps that contained snails, three were sampled quantitatively, two in the main part of the Narrows and one in Orderville Canyon. The first seep was 4 m wide, located approximately 0.3 km into the Narrows, and had a density of 30 snails/m^2. The second was 6 m wide, located 0.5 km into the Narrows, and had approximately 100 snails/m^2. The seep in Orderville Canyon is a long, continuous dripline with approximately 130 snails/m^2. The other three seeps that contained snails were in the main part of the Narrows. These seeps were all less than 3 m wide and had estimated densities of $<$ 20 snails/m^2. The largest snails, 6.5 to 7.0 mm in length, were found in the main Narrows. Average length ranged from 3.0 to 6.0 mm (Fig. 1). Based on the above densities, 3,000 snails is a conservative estimate of the minimum population in the Narrows region.

GATEWAY.—This area was only qualitatively sampled because the large number of park visitors using the trail made quantitative sampling impractical. Very few seeps contained snails, and even in large or continuous seeps the snails were found in discrete patches. Densities of 5 to 10 snails/m^2 were common, with 20 to 30 snails/m^2 maximum. Snail sizes throughout this area were 3 to 4 mm at the time of sampling.

MAIN CANYON.—The only snails found in the Main Canyon area were in a terraced seep-spring 1.0 km north of Scout Lookout. Three in-seep snail distributional patterns were evident: (1) on the terraces of the seep; (2) at the head of the northern-most spring; and (3) in the main stream below the waterfall down to the confluence with the Virgin River. Snails were not found in the southern spring. Densities ranged from 40/m^2 in the stream to more than 250/m^2 in the spring. However, because of the small surface area of the spring, the total number of snails there is less than 1,000. The highest densities were found in spring season with the appearance of young snails. In the terrace region the density was around 175/m^2. The size ranged from $<$ 1.0 mm (immatures) to 4.0 mm. Snails $>$ 5.0 mm were rare in this area. There was a marked decrease of snails $>$ 3.5 mm after June. The total population in this area apparently ranged from 2,000 to 6,000 snails.

Table 2. Results of natural substrate wash experiment using in situ *Physa zionis*.

Duration (Seconds)	Volume (Liters)	Rate of flow	Replicates	Number of snails Start	Number of snails Finish	Percent remaining
5	5	1 l/sec	1	16	13	81.25
			2	11	8	72.72
			3	12	11	91.66
			4	13	11	84.62
	10	2 l/sec	1	10	10	100.00
			2	10	7	70.00
			3	10	7	70.00
			4	12	9	75.00
10	5	0.5 l/sec	1	12	12	100.00
			2	12	12	100.00
			3	13	7	53.85
			4	13	12	92.31
	10	1 l/sec	1	12	10	83.33
			2	11	9	81.81
			3	11	9	81.81
			4	14	12	85.71

Wash Experiments

In the preliminary plastic channel test, eight snails were used. At the initial flow of water through the channel, two snails were lost; the others remained attached up to flows of 280 mm in the measuring tube, the maximum achievable using water available in the field. Size did not appear to be a factor in attachment ability, since the largest (5 mm) and the smallest (1.5 mm) were among those remaining.

In the natural-substrate wash experiment, 78% of the snails remained attached after the highest flow (10 liters for 5 sec = 2 l/sec), and 86% remained after the lowest flow (5 liters for 10 sec = 0.5 l/sec). With flows of 1 l/sec, 83% remained after 5 and 10 sec. durations (Table 2). Snails became detached when the carbonate or sandstone substrate they were on washed away.

Physa gyrina, a coiled shell gastropod that was common in the area, was tested in the laboratory for comparison with the attachment ability of the Zion Snail. In the preliminary plastic channel test, only two snails remained after the initial flow of water. At < 75 mm of flow in the measuring tube, the shells of the remaining snails started to lift from the foot and soon pulled the foot off the channel. No snails remained in the plastic channel after flows of > 75 mm. In the controlled wash experiment, only 2 of 16 and 1 of 12 snails remained at 5 liters and 10 seconds (0.5 l/sec), the lowest flow possible. A third replicate with 12 snails left no snails remaining, and the experiment was stopped.

Within Seep Distribution

The seep-spring area was chosen for the analysis of factors that influence local distributions. Snails were found in 126 of 262 quadrats (48.1%). Using a Chi-square test of independence, snail distribution was found to be independent of slope and algae cover while dependent on depth and flow (Table 3). Flow class 1 (<1 mm) accounted for 125 of the 126 quadrats (99.2%) that contained snails. The proportion of quadrats that contained snails also decreased with increasing water depth. The single quadrat with a snail in high flow (> 1 mm) is not significantly different from 0 (Table 4).

In an attempt to determine the overall effects of the variables and their interactions on snail distribution, the ANOVA model

$$Y \text{ (snails)} = D \text{ (depth)} + V \text{ (velocity)} + S \text{ (slope)} + DV + DS + VS + E$$

was used in weighted least squares analysis in RUMMAGE. Algal cover was not used because it was not significant and the five cover classes were contributing too many missing cells. The data used were from a single sampling date and from a specific area in the seep-spring to minimize effects of unaccounted factors. The three factors plus interactions accounted for 19% of the variation ($R^2 = 0.193$, R^2 adj. for df = 0.101). The terms *water depth* and *velocity* were significant at $p < 0.05$ (Table 5).

TABLE 3. Chi-square analysis of independence to determine the significance of water depth, water flow (velocity), substrate slope, and algal cover in determining the distribution of the Zion Snail in the seep-spring area.

Variable	x^2	df	Significance
Depth*	33.78	2	**
Flow	19.33	1	**
Slope	0.50	2	N. S.
Algae	2.10	4	N. S.

*Depth class 4 was added to 3 since less than five samples were taken at depths greater than 10 mm.
**$p < 0.05$

TABLE 4. Number of quadrats and occurrence of snails within various water depth and flow categories.

Parameter[a] and category		N	# with Snails (% ± 95% C. I.)
Depth[b]	1	142	90 (63.4 ± 7.9)
	2	74	28 (37.8 ± 11.1)
	3	46	8 (17.4 ± 11.0)
Flow	1	239	125 (52.3 ± 6.3)
	2	23	1 (4.3 ± 8.3)[c]

[a] See Table 1 for description.
[b] Depth class 4 was added to 3 since less than five samples were taken at depths greater than 10 mm.
[c] Not significantly different from 0 at $p < 0.05$.

DISCUSSION

The highest population densities were found in Orderville Canyon and the seep-spring. Both areas had densities exceeding $100/m^2$. Early accounts of the snail did not include density estimates; consequently, historic comparisons cannot be made. However, Gregg (1940) described "Fairy Land" 3/4 mi south of Sinawava as a terraced region with numerous snails on horizontal surfaces. From his description and the location, Fairy Land is possibly the seep-spring area we studied. Pilsbry (1926) collected the type specimens at the Narrows mouth and found no Zion Snails above three miles into the Narrows. Because of accessibility, Zion Snails were often collected at the mouth of the Narrows. Woodbury (cited in Chamberlain and Jones 1929: 167) reported that cliffs (seeps) near the type locality and beyond had been "stripped of snails by collectors on previous occasions, but that in a few days migration from above had soon renewed the supply." The migration reported is most likely of snails from higher, inaccessible parts of the seep to the lower regions visited by collectors. Presently, the lower, accessible seeps in the Gateway and the mouth of the Narrows contribute only a small percentage to the total number of Zion Snails in the park.

The distribution of the Zion Snail is patchy. They occur at differing distances in reference to the Virgin River, with various distances between subpopulations. The only snails found in deep water were those in the stream below the waterfall at the seep-spring area. However, density in the stream was very low and most likely was the result of snails being washed down from the seep above.

The silt-laden Virgin River, despite being the physical factor that joins most of the seeps together, may be a barrier to snail movement and contributes to the patchy distribution. The absence of snails in the river's main channel may indicate an avoidance of the silt or an inability to survive there. However, the river may still be a major avenue of dispersal. Some snails in the Narrows occur very close to the river and may be carried downstream during highwater or flooding. These snails are certainly covered during periods of high flow. If the snail can survive in the river for a short period of time, the Narrows may be a source of its origin for downstream areas. The seeps along the Gateway that are presently isolated from the river may have been colonized during extreme flooding or by other vectors. The extreme patchiness may be a reflection of rare colonization events and local extinction.

Within seeps, the snail distribution is patchy. Water depth and velocity are viewed as limiting factors on a gross scale. Snails are found in decreasing frequencies with increasing water depth and are not found at all in areas of high flow (Table 4). However, as shown by the ANOVA model, depth and water velocity only accounted for 10% of the variation when adjusted for df. Even in areas of favorable depth and velocity, much of the distributional variation is unexplained by the measured factors. The localized patchiness may be linked with food sources, variations in water flow, and the movement of snails that were not measured.

As shown by the flow experiments, the Zion Snail is suited for living in water flows much higher than those normally encountered in the seeps. The attachment abilities are also much greater than *Physa gyrina*, which has a

TABLE 5. Results of RUMMAGE ANOVA testing occurrence of snails with environmental variables Depth (D), Flow (F) and Slope (S). (N = 262).

Source	df	ss	MS	F	Significance
D	3	31.70	10.58	4.32	0.006
F	1	24.52	24.52	10.02	0.002
S	2	0.72	0.36	0.15	0.863
DF	2[a]	8.80	4.40	1.80	0.169
DS	6	15.25	2.54	1.04	0.403
FS	2	8.62	4.31	1.76	0.175
Error	141	345.05	2.45		

$R^2 = 0.193$

R^2 adjusted for df = 0.101

[a] df lost due to missing cell.

higher, coiled shell. The early literature (Pilsbry 1926, Woodbury 1929, Chamberlain and Jones 1929) states that the purpose of the limpetlike shell and large foot is to allow the snail to live on the vertical surfaces in the trickling water. However, most snails are not found in visibly moving water and are not restricted to vertical surfaces. Slope was not a significant factor (Table 5), and snails are found on horizontal surfaces.

The hypothesis (Woodbury 1933) that the large foot and reduced spire evolved from a more typical physoid type snail as a result of high flows or floods in the seep environment is probably correct. We feel the selective value of attachment during high flows is quite significant. Seeps near the river are occasionally flooded (Malanson 1978), and the ability to remain attached during floods would be an advantage. Based on the experiments, the higher, coiled shell of a typical snail would have caused it to be washed away even in a minor flood, whereas a majority of the Zion Snails would have remained attached to the seep. The adaptive value to the Zion Snail of a large foot and limpetlike shell is, in our opinion, to remain attached during periods of fast flows and flooding, allowing the snail to remain in and exploit seep habitats.

SUMMARY

This research, along with past studies on the Zion Snail, provides a basic understanding of its general distribution and habitat use. Future studies should be done to determine the distribution further up the Narrows and in Orderville Canyon; the role of temperature in controlling reproduction, food habits, and mortality factors; the role of drying seeps on distribution; and, finally, the effect of floods on the Narrows and Orderville Canyon populations. Some of these proposed studies would necessitate collecting adult snails and raising them in the laboratory, but others could only be accomplished after long-term field observations. Lastly, it must be recognized that we know nothing of populations in gardens high up on the canyon wall or if the snail even exists in those gardens.

Although the snail is endemic to Zion National Park, there are no large populations, but the populations we studied contained sufficient numbers for reproduction to take place. The Zion Snail has probably never existed in large numbers and, in comparison to other snails, it may be considered rare.

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BLOCKAGE AND RECOVERY OF NITRIFICATION IN SOILS EXPOSED TO ACETYLENE[1]

Steven J. Burns[2,3] and Richard E. Terry[2]

ABSTRACT.—Acetylene gas is very useful in laboratory and in situ assay procedures for nitrogen fixation and denitrification. There is concern, however, that measurements of denitrification may be underestimated because nitrification, a major source of nitrate, is inhibited by C_2H_2. The objective of this study was to examine the effects of C_2H_2 partial pressure and length of exposure time on nitrification in soils. Acetylene partial pressures of 0.1, 1.0, and 10.0 kPa were found to effectively inhibit nitrification in soil samples incubated in the laboratory. Both the partial pressure of C_2H_2 and the length of exposure time were found to affect the recovery time of nitrification in soil samples. Nitrification recovered within seven days in samples exposed to 0.1 and 1.0 kPa C_2H_2 for only 24 hours. The recovery of nitrification in samples exposed to 10.0 kPa C_2H_2 for 24 hours or to 0.1 and 1.0 kPa C_2H_2 for 216 hours was delayed for an additional seven days, however.

Acetylene gas has been effectively used in laboratory and in situ techniques for the measurement of both nitrogen fixation and denitrification. The use of acetylene (C_2H_2) is attractive due to the low cost and high sensitivity of the procedures. For N_2 fixation studies, C_2H_2 is used to saturate enzymes responsible for fixation; in the process, C_2H_2 is reduced to ethylene (C_2H_4). Ethylene can be readily detected by gas chromatography and N_2 fixation rates estimated (Hardy et al. 1968, Bergerson 1980). Acetylene has an inhibitory effect on the bacterial enzymes that reduce N_2O to N_2; therefore, C_2H_2 has been used in denitrification studies (Balderson et al. 1976, Yoshinari et al. 1977). In the presence of C_2H_2 partial pressures greater than 0.1 kPa, N_2O is the sole gaseous product of denitrification and is detectable by gas chromatography.

Concerns have been expressed about the use of C_2H_2 in denitrification studies, because C_2H_2 has been found to be an effective nitrification inhibitor at a partial pressure of 0.01 kPa (Walter et al. 1979, Berg et al. 1982). In some situations denitrification measurements may be affected by C_2H_2, because nitrification, a major source of NO_3^-, is inhibited. This is not a problem with short-term laboratory incubations or experiments that involve the addition of nitrate to the soil, but it may be inappropriate to use acetylene in experiments where NH_4^+ is used as the starting point in denitrification studies or in long-term experiments where mineralization and subsequent nitrification could be expected to produce significant nitrate.

Researchers have studied nitrification in the presence of C_2H_2 partial pressures ranging from 1,000 to 0.01 Pa (Walter et al. 1979, Berg et al. 1982). The minimum effective partial pressure that inhibited nitrification was 10 Pa. However, partial inhibition was found at 0.1 Pa (Berg et al. 1982). These researchers reported that the inhibitory effects of the low C_2H_2 levels (1,000 to 10 Pa) ceased within 7 to 10 days of removal of C_2H_2.

Acetylene partial pressures of 10 kPa are routinely used in nitrogen fixation studies (Hardy et al. 1968, Bergerson 1980) and in laboratory denitrification studies (Yoshinari et al. 1977, Terry and Tate 1980a, 1980b, Terry et al. 1981). Field measurement of denitrification by the C_2H_2 inhibition technique involves introduction of C_2H_2 to the soil atmosphere through perforated tubing or C_2H_2 treated irrigation water (Ryden, *I., Laboratory evaluation*, 1979; Ryden, II., *Development and application*, 1979, Rolston et al. 1982, Hallmark and Terry 1985). It is likely, with these procedures, that C_2H_2 partial pressures in excess of 10 kPa will exist in portions of the soil atmosphere that will maintain minimum effective levels of 0.1 kPa throughout the soil atmosphere.

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[1] This publication is based on work supported in part by funds provided by the Bureau of Land Management.

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TABLE 1. The properties of soils used in this investigation.

Soil series	pH	Sand	Silt	Clay	Organic-C	Total-N
		g kg^{-1}				
Timpanogos	7.9	348	309	343	12.5	1.27
Woodrow	8.1	239	390	375	8.8	1.40

The effects of C_2H_2 partial pressures greater than 1 kPa on nitrification and the resumption of nitrification following exposure have not been studied. The objective of this research was to determine the effects of various C_2H_2 partial pressures and length of C_2H_2 exposure time on nitrification in soils.

MATERIALS AND METHODS

Soils used in this investigation were Timpanogos clay loam (a fine, loamy, mixed mesic Calcic Argixeroll) collected at the Brigham Young University Agriculture Station near Spanish Fork, Utah, and Woodrow clay loam (a fine silty, mixed mesic Xeric Torrifluvent), collected at Camp Floyd State Park, Fairfield, Utah. The properties of the soils used in this study are presented in Table 1. Air-dried soil samples were analyzed for total N by the micro-Kjeldahl method of Bremner (1965) and for organic C by the method of Allison (1965). The soil pH was measured by glass electrode on a 1:1 soil:water ratio.

Duplicate moist soil samples, the equivalent of 10.0 g dry weight, were placed into 120 ml serum bottles and sealed with septum stoppers. The samples were brought to approximately −0.333 MPa matric potential by addition of 1.25 ml of a solution containing 3.96 g $(NH_4)_2$ SO_4 L^{-1} to equal an application rate of 100 mg N kg^{-1} soil. The soils were preincubated for 24 hours before treatment with C_2H_2.

To compare the inhibitory effects of various levels of C_2H_2 with those of the commercial nitrification inhibitor, nitrapyrin, soil samples were continuously exposed to C_2H_2 partial pressures of 0.1, 1.0 or 10.0 kPa. Impurities were removed from C_2H_2 by passage of the gas through concentrated H_2SO_4 and water traps (Hardy et al. 1968). Nitrapyrin was dissolved in the ammonium solution and added to the soil samples at the rate of 2 mg kg^{-1}. The continuously exposed samples were unsealed, aerated for 10 minutes once a week, then reexposed to acetylene, thus eliminating anaerobic conditions. Nitrapyrin samples were also aerated for 10 minutes once a week.

To examine the effects of various partial pressures of acetylene on nitrification and the recovery of nitrification following exposure, acetylene was added at rates of 0, 0.1, 1.0, and 10.0 kPa for a period of 24 hours and then removed by flushing the incubation vessels with air. The samples were then incubated at 21 C and continuously aerated with laboratory air at 100% relative humidity using a manifold delivery system and an aquarium air pump. The air flow rate for each sample was 0.5 mL s^{-1}.

To determine the effects of length of acetylene exposure time on nitrification, soil samples were exposed to 0.1, 1.0, or 10.0 kPa C_2H_2 for 24 or 216 hours. Following exposure, acetylene was removed by flushing with air and the samples were then continuously aerated.

Sufficient samples were prepared to allow for duplicate analyses at 0, 7, 14, 21, and 28 days. At the end of incubation inorganic N was extracted from the samples with 50 mL of 2M KCl and NH_4^+, NO_2^-, and NO_3^- were determined by the steam distillation procedure of Bremner and Keeney (1965).

RESULTS AND DISCUSSION

The effectiveness of C_2H_2 and the commercial nitrification inhibitor, nitrapyrin, on inhibition of nitrification in Timpanogos clay loam was tested. Nitrapyrin, and C_2H_2 at partial pressures ranging from 0.1 to 10.0 kPa, effectively inhibited nitrification in this soil throughout the 28-day incubation (Table 2). The soil samples were preincubated for 1 day to allow the $(NH_4)_2SO_4$ or $(NH_4)_2$ SO_4 + nitrapyrin solutions to equilibrate with the soil prior to C_2H_2 addition and incubation. The difference in the NH_4^+-N levels between the nitrapyrin and C_2H_2 treatments at day 0 indicated that approximately 20% of the added

TABLE 2. The effects of various acetylene partial pressures and nitrapyrin on nitrification in Timpanogos clay loam.

C_2H_2 Partial pressure #	Form of N	Days of incubation 0	7	14	21	28
kPa		Inorganic N mg kg^{-1}				
0.1	NH_4^+	79	79	82	83	81
	$NO_3^- + NO_2^-$	60	62	60	61	60
1.0	NH_4^+	80	81	83	84	84
	$NO_3^- + NO_2^-$	60	61	62	61	62
10.0	NH_4^+	80	80	81	84	87
	$NO_3^- + NO_2^-$	59	61	61	59	61
NITRAPYRIN	NH_4^+	98	95	97	97	n.d.*
	$NO_3^- + NO_2^-$	55	51	56	53	n.d.*

*n.d. = not determined
#Except Nitrapyrin

TABLE 3. The effects of a 24-hour exposure to C_2H_2 partial pressures ranging from 0 to 10 kPa on nitrification in Timpanogos cl.

C_2H_2 Partial pressure	Form of N	Days of incubation 0	7	14	21	28
kPa		Inorganic N mg kg^{-1}				
0	NH_4^+	52	0	0	0	0
	$NO_3^- + NO_2^-$	83	140	147	148	150
0.1	NH_4^+	78	0	0	0	0
	$NO_3^- + NO_2^-$	61	146	146	152	148
1.0	NH_4^+	70	0	0	0	0
	$NO_3^- + NO_2^-$	63	144	144	152	156
10.0	NH_4^+	68	45	2	0	0
	$NO_3^- + NO_2^-$	63	93	140	150	155

NH_4^+-N was nitrified during preincubation. The finding that C_2H_2 partial pressures ranging from 0.1 to 10.0 kPa inhibited nitrification concurred with earlier work of Walter et al. (1979) and Berg et al. (1982), who showed that C_2H_2 partial pressures of 1.0 and 0.1 kPa effectively inhibited nitrification in soils.

The effects of 24 hours of exposure to C_2H_2 partial pressures ranging from 0 to 10.0 kPa on subsequent changes in NH_4^+-N and $(NO_3^- + NO_2^-)-N$ concentrations in the Timpanogos soil are shown in Table 3. The zero time of incubation followed the 24-hour preincubation and the 24 hours of exposure of C_2H_2. Nitrification continued in the control samples (0 kPa) during the 24-hour period that the remaining treatments were exposed to C_2H_2. For this reason more $(NO_3^- + NO_2^-)-N$ had accumulated in the control samples during preincubation. During the first week if incubation following removal of C_2H_2, nitrification of added NH_4^+-N was complete in all samples except those treated with 10.0 kPa. Nitrification in the samples exposed to 10.0 kPa C_2H_2 for 24 hours was slowed for approximately two weeks due to the lingering effects of acetylene exposure. There were no differences in the NH_4^+-N and $(NO_3^-+NO_2^-)-N$ concentrations during incubation of the 0.1 and 1.0 kPa treatments. During the first week following removal of C_2H_2 from the samples, the nitrification rate in samples exposed to 0.1 and 1.0 kPa C_2H_2 was 12 mg N kg^{-1} day^{-1} compared to 4.3 mg N kg^{-1} day^{-1} in those treated with 10 kPa.

Samples of the Woodrow clay loam were incubated aerobically following a 24-hour exposure to, and subsequent removal of, C_2H_2 partial pressures ranging from 0 to 10.0 kPa. The effects of this brief exposure on subsequent changes in NH_4^+-N and $(NO_3^-+NO_2^-)-N$ concentrations are shown in Table 4. During the first week following C_2H_2 removal, the nitrification rates for 0, 0.1, 1.0, and 10.0 kPa C_2H_2 treatments were 5.2, 5.7, 2.1, and 3.6 mg N kg^{-1} day^{-1}, respectively. Accumulation of $(NO_3^-+NO_2^-)-N$ in the samples exposed to 1.0 and 10.0 kPa was slower during the first week of incubation.

Nitrification proceeded in the Woodrow cl, an unfertilized rangeland soil, at a slower pace

TABLE 4. The effects of a 24-hour exposure of C_2H_2 partial pressures ranging from 0 to 10 kPa on nitrification in Woodrow cl.

C_2H_2 Partial pressure	Form of N	Days of incubation 0	7	14	21	28
kPa		Inorganic N mg kg^{-1}				
0	NH_4^+	79	31	0	0	0
	$NO_3^- + NO_2^-$	19	56	105	106	114
0.1	NH_4^+	87	54	5	0	0
	$NO_3^- + NO_2^-$	12	52	98	104	111
1.0	NH_4^+	83	70	19	0	0
	$NO_3^- + NO_2^-$	12	27	82	101	111
10.0	NH_4^+	83	62	18	2	0
	$NO_3^- + NO_2^-$	13	38	83	93	110

TABLE 5. The effects of C_2H_2 partial pressure and length of exposure time on nitrification in Timpanogos cl.

C_2H_2 Partial pressure	Exposure time	Form of N	Days of incubation 0	7	14	21	28
kPa	Hours		Inorganic N mg kg^{-1}				
10	24	NH_4^+	68	45	2	0	0
		$NO_3^- + NO_2^-$	63	93	140	151	155
	216	NH_4^+	81	48	1	0	0
		$NO_3^- + NO_2^-$	59	89	149	149	148
1.0	24	NH_4^+	70	0	0	0	0
		$NO_3^- + NO_2^-$	63	144	145	153	156
	216	NH_4^+	81	47	1	0	0
		$NO_3^- + NO_2^-$	60	95	139	148	158
0.1	24	NH_4^+	78	0	0	0	0
		$NO_3^- + NO_2^-$	61	146	146	153	148
	216	NH_4^+	80	47	1	0	0
		$NO_3^- + NO_2^-$	61	94	148	152	158

than in the Timpanogos cl, a fertilized cropped soil. The results reported above indicate that brief exposure (24 hours) to C_2H_2 partial pressures ranging from 0.1 to 1.0 kPa have little effect on nitrification in these soils. Brief exposure of soil to 10.0 kPa C_2H_2 slowed subsequent nitrification for as long as two weeks, however.

The effects of length of C_2H_2 exposure time on recovery of nitrification in Timpanogos cl are shown in Table 5. Nitrification rates in soil samples treated with 10.0 kPa acetylene were equivalent during the first week of incubation following C_2H_2 removal whether exposed to the gas for 24 or 216 hours. Nitrification was nearly complete within one week in samples exposed to 0.1 or 1.0 kPa for only 24 hours. Nitrification rates in samples exposed to 0.1 and 1.0 kPa C_2H_2 for 216 hours were much slower, however. The effects of lengthy exposure (216 hours) to C_2H_2 partial pressures of 0.1 and 1.0 kPa on subsequent nitrification were similar to the effects of brief exposure (24 hours) to 10.0 kPa.

Walter et al. (1979) reported that nitrification rates in soil samples exposed to C_2H_2 partial pressures ranging from 0.1 to 1.0 kPa for 24 hours returned to those of control samples after an 8 to 10 day lag period. Similar results were reported by Berg et al. (1982), who exposed soil samples to 0.01 kPa C_2H_2 for seven days. They reported that rates of nitrate production were similar to the rates in control samples seven days after C_2H_2 removal.

The findings of this experiment indicate that both the partial pressure of C_2H_2 and the length of exposure time affect the recovery time of nitrification in soil samples. Exposure of Woodrow cl to 0.1 and 1.0 kPa C_2H_2 for 24 hours slowed nitrification for approximately seven days. Exposure of Timpanogos cl to 0.1 and 1.0 kPa C_2H_2 for 24 hours had little effect on nitrification once the inhibitor was removed. Exposure of this soil to 0.1 and 1.0 kPa acetylene for 216 hours slowed nitrification for approximately seven days, however. These levels of C_2H_2 exposure are commonly used in laboratory and in situ denitrification studies (Yoshinari et al. 1977, Ryden, *II., Development and application*, 1979; Rolson et al. 1982, Ryden and Dawson 1982). The recovery of nitrification in Timpanogos soil exposed to 10.0 kPa C_2H_2 was delayed for at least seven days whether the samples were exposed to the gas for 24 or 216 hours. Acetylene partial pressures of 10.0 kPa have been used in denitrification studies and in studies of concurrent denitrification and nitrogen fixation (Terry and Tate 1980a, 1980b, Yoshinari et al. 1977).

Problems with the use of C_2H_2 in denitrification studies would likely be encountered in soils where the nitrate supply is limited by nitrification. Ryden (1982) reported that denitrification was underestimated in soil samples incubated in the laboratory in the presence of C_2H_2 for 168 hours. Nitrate became exhausted in the samples during incubation. Problems with nitrification inhibition in denitrification studies may be avoided in laboratory studies by adding supplemental nitrate and/or adopting short incubation periods (<24 hours) (Terry and Tate, 1980b). In the design of field studies on denitrification, it would be wise to rotate study sites every 7 to 14 days to allow nitrification to proceed in the soil. The use of sites previously exposed to C_2H_2 should be avoided for 14 to 21 days because of the slow recovery of nitrification following prolonged exposure to C_2H_2.

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NEW THAGRIINE LEAFHOPPERS FROM THE ORIENTAL REGION, WITH A KEY TO 30 SPECIES (HOMOPTERA: CICADELLIDAE: COELIDIINAE)

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Abstract.—Five new species of *Thagria* from the Oriental region are described and illustrated. These include *melichari* from Thailand, *unidentata* from Indonesia, *marissae* from southern China, *bifida* from Nepal, and *insolentis* from an undetermined locality in the Oriental region. There are presently 166 species in this large and unique genus. A key to males of 30 species is included.

The genus *Thagria* Melichar is the largest group of coelidiine leafhoppers. Although they occur primarily in the Oriental region, many species are found in the Australian region (not known in Australia proper) and several are in the southern Palearctic region (southern China, southern Korea, and southern Japan). Prior to 1977 only 36 species were known. Since then 125 species have been described (Kwon and Lee 1979, Nielson 1977, 1980a, 1980b, 1980c, 1980d, 1982). The five new species described herein bring the present total to 166 species.

The genus is uniquely characterized by the males possessing a distinctive and highly diverse ventral paraphysis on which a tubular aeadeagal shaft is attached basally to and freely articulates dorsally with the paraphysis. The many configurations of the ventral paraphysis in combination with highly modified structures of the 10th segment and caudodorsal processes of the pygofer differentiate the numerous species.

A key to males of 30 species including those described in previous papers (except Kwon and Lee 1979) after my 1977 revision and those treated herein is presented. A regional key for all known species will be presented later.

Host plants and biology of species in the group are very poorly known.

Key to Males of *Thagria*

1. Clypellus broad, swollen basally or nearly so, basal width equal to or greater than basal width of clypeus, lateral margins usually narrowed medially 2

— Clypellus narrow, never swollen basally, basal width narrower than basal width of clypeus, lateral margins usually parallel, sometimes expanded distally 16

2(1). Ventral paraphysis curved ventrally at distal 1/2 to 1/3 in lateral view, apex decurved 3

— Ventral paraphysis not as above, in lateral view straight or recurved 5

3(2). Style with apex bifurcate or divided into 2 slender rami 4

— Style not as above (Fig. 16, Nielson 1980a) .. .. *blockeri* Nielson

4(3). Aedeagus long, extending beyond midlength of ventral paraphysis; 10th segment process with dentate process on middle of dorsal margin (Fig. 2) .... *bifida*, n. sp.

— Aedeagus shorter, reaching to about midlength of ventral paraphysis; 10th segment process with longer process on ventral margin (Fig. 25, Nielson 1980b) . *thailandensis* Nielson

5(3). Ventral paraphysis symmetrical 6

— Ventral paraphysis asymmetrical 10

6(5). Tenth segment with paired processes 7

— Tenth segment without paired processes (Fig. 13, Nielson 1980b) .... *ampla* Nielson

7(6). Ventral paraphysis without basal paired processes on dorsal margin 8

— Ventral paraphysis with basal paired processes on dorsal margin (Fig, 22, Nielson 1980b) .... *serrastyla* Nielson

8(7). Style very long, exceeding midlength of ventral paraphysis; ventral paraphysis without spines distally 9

— Style very short, not reaching midlength of ventral paraphysis; ventral paraphysis with lateral spines distally (Fig. 28, Nielson 1982) .... *barbata* Nielson

9(8). Style attenuated distally (Fig. 2, Nielson 1982) .... *fossiata* Nielson

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— Style forked distally (Fig. 11, Nielson 1980c) . . . . *furculata* Nielson

10(5). Ventral paraphysis with basal processes on dorsal margin 11

— Ventral paraphysis without basal processes but with medial or subapical processes on dorsal margin 14

11(10). Ventral paraphysis with paired basal processes 12

— Ventral paraphysis with single basal process. 13

12(11). Basal processes on paraphysis symmetrical (Figs. 11,12) . . . . *melichari*, n. sp.

— Basal processes on paraphysis asymmetrical (Fig. 40, Nielson 1982) . . . . . *hollowayi* Nielson

13(11). Style broad throughout in dorsal view, without dentate subapical processes (Fig. 39, Nielson 1980b) . . . . *boulardi* Nielson

— Style narrowed at distal 1/4 in lateral view, with dentate subapical process (Fig. 35, Nielson 1980b) . . . . *paraornata* Nielson

14(10). Tenth segment and caudodorsal margin of pygofer with processes of equal length in lateral view; ventral paraphysis with short lateral process distad of middle 15

— Tenth segment and caudodorsal margin of pygofer with processes of unequal length in lateral view; ventral paraphysis with short lateral process on middle (Fig. 4, Nielson 1980b) . . . . *undulata* Nielson

15(14). Tenth segment processes very narrow and sinuate, nearly needlelike at distal 2/3 in dorsal view (Fig. 8, Nielson 1980b) . *capilla* Nielson

— Tenth segment processes broader and nearly straight, not needlelike in dorsal view (Fig. 20, Nielson 1980a) . . . . *paradigitata* Nielson

16(2). Ventral paraphysis symmetrical 17

— Ventral paraphysis asymmetrical 25

17(16). Ventral paraphysis keeled ventrally 18

— Ventral paraphysis not as above 20

18(17). Ventral paraphysis with subbasal ventral keel 19

— Ventral paraphysis with subapical ventral keel (Fig. 10, Nielson 1980d) . *paraloae* Nielson

19(18). Style very long, extending beyond apex of ventral paraphysis (Fig. 22, Nielson 1980d) . . . . *samuelsoni* Nielson

— Style very short, extending only to base of ventral paraphysis (Fig. 3, Nielson 1980c) . . . . *ventrocarina* Nielson

20(17). Ventral paraphysis with paired basal process on dorsal margin 21

— Ventral paraphysis not as above 22

21(20). Paired basal processes of paraphysis very long, nearly reaching to apex of paraphysis (Fig. 3, Nielson 1980d) . . . . . *bilateralis* Nielson

— Paired basal processes of paraphysis shorter, not reaching midlength of paraphysis (Figs. 16, 17) . . . . *insolentis*, n. sp.

22(20). Caudoventral lobe of pygofer without spines 23

— Caudoventral lobe of pygofer with 2 short spines apically (Fig. 7, Nielson 1982) . . . . *bidentata* Nielson

23(22). Ventral paraphysis without lateral processe 24

— Ventral paraphysis with lateral processes subapically (Fig. 3, Nielson 1980a) . . . . *srilankensis* Nielson

24(23). Style with subapical bifurcation (Fig. 21, Nielson 1982) . . . . *bifurcata* Nielson

— Style without subapical bifurcation (Fig. 11, Nielson 1980a) . . . . *brincki* Nielson

25(16). Style with distal half straight or nearly so . . . 26

— Style with distal half hooked (Fig. 17, Nielson 1980d) . . . . *paraexilis* Nielson

26(25). Ventral paraphysis without ventral keel 27

— Ventral paraphysis with ventral keel subbasally (Fig. 17, Nielson 1982) . . . . *mutabilis* Nielson

27(26). Ventral paraphysis with 1–2 lateral processes on or near apex 28

— Ventral paraphysis without such processes . . 29

28(27). Ventral paraphysis with a pair of unequal distal processes (Fig. 23) . . . . *marrisae*, n. sp.

— Ventral paraphysis with a single, large, retrorse lateral process subapically (Fig. 35, Nielson 1982) . . . . *retrorsa* Nielson

29(27). Caudoventral lobe of pygofer with a single long spine (Fig. 26) . . . . *unidentata*, n. sp.

— Caudoventral lobe of pygofer without such spine (Fig. 13, Nielson 1980c) . . . . *kaloostiani* Nielson

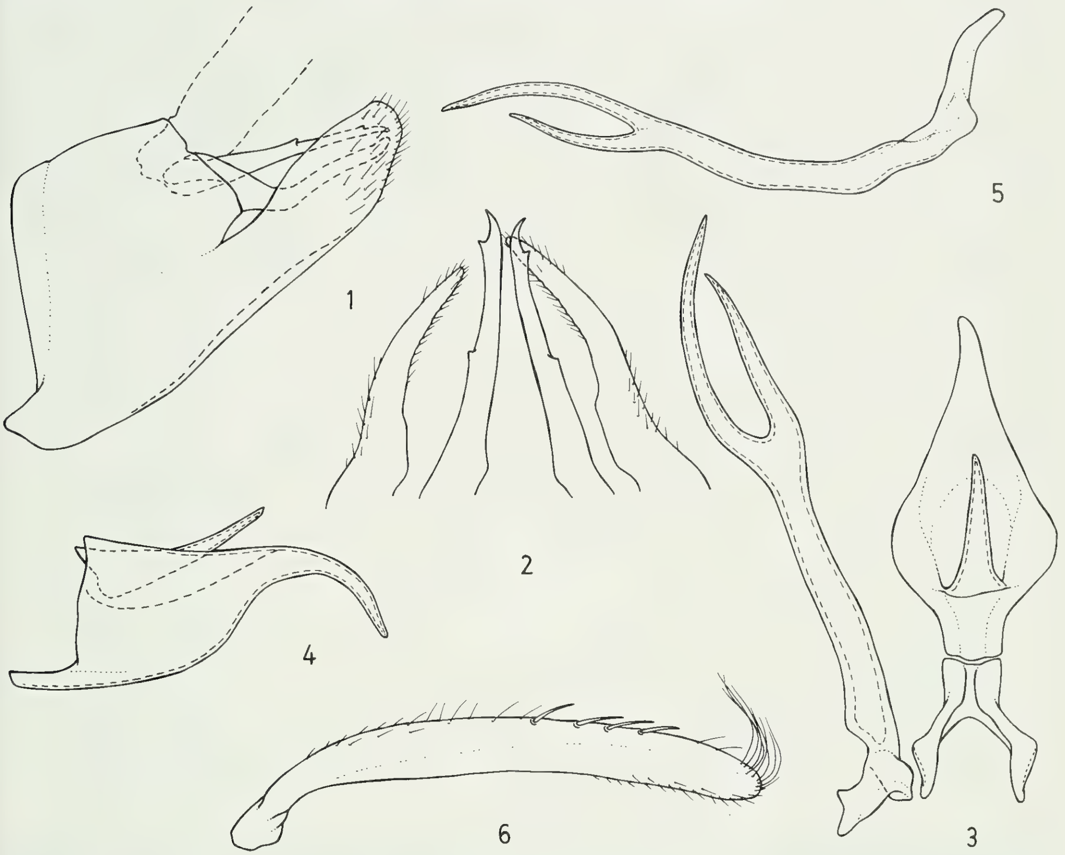
Thagria bifida, n. sp.

Figs. 1–6

LENGTH: Male 6.90 mm.

Moderate-sized, slender species. General color black with tannish translucent costa, face black.

Head small, subconical, much narrower than pronotum; crown broad, width about equal to width of eyes, produced beyond anterior margin of eyes, elevated above level of eyes, lateral margins convergent basally; eyes moderately large, semiglobular; pronotum with length about equal to length of crown; scutellum large; forewings long and narrow, venation typical of genus; clypeus long and broad, lateral margins excised near middle; clypellus short and broad, base broad and swollen, lateral margins below converging to truncate apex.



Figs. 1–6. *Thagria bifida*: 1, Male pygofer and 10th segment, lateral view. 2, Tenth segment, and pygofer processes, dorsal view. 3, Connective, aedeagus, ventral paraphysis and right style, dorsal view. 4, Aedeagus and ventral paraphysis, lateral view. 5, Right style, lateral view. 6, Plate, ventral view.

MALE: Pygofer in lateral view with rather long, broad, caudoventral lobe, apex narrowly rounded; caudodorsal margin with long, narrow, slightly sinuate process, nearly reaching apex of caudoventral lobe (Fig. 1); 10th segment with pair of long slender acuminate processes nearly reaching to apex of anal tube, processes with 2 small dentate projections, one subapical and one near middle on dorsal margin (Figs. 1, 2); aedeagus symmetrical, long, extending beyond midlength of ventral paraphysis (Fig. 3); ventral paraphysis short, very broad at basal half in dorsal and lateral views, narrowed at distal half and decurved in lateral view (Figs. 3, 4); style very long, extending beyond apex of ventral paraphysis, bifurcate subapically, inner bifurcation shorter than outer one (Fig. 3); plate long and narrow with few lateral macrosetae and few short microsetae apically (Fig. 6).

HOLOTYPE (male): NEPAL: Ktmd. [Katmandu], Pulchauki, 8000′, 27.VII. 1967. Can. Nepal Exp. (CNC)

REMARKS: This species is similar to *obrienae* Nielson but can be distinguished by the diagnostic bifurcate style.

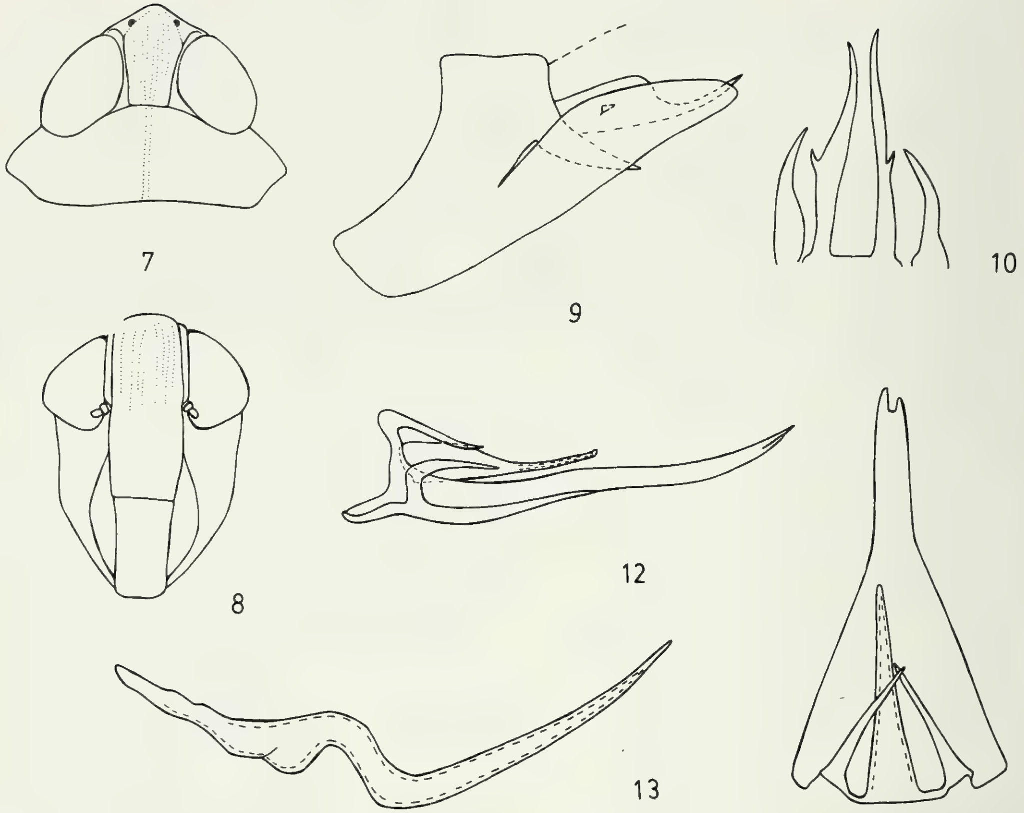
Thagria melichari, n. sp.

Figs. 7–13

LENGTH: Male 6.60 mm.

Moderately robust species. General color ochraceous with narrow transverse ivory markings on forewings, veins embrowned with small irregular ochraceous spots, on veins.

Head much narrower than pronotum (Fig. 7); crown narrow, produced distally beyond anterior margin of eyes, length twice basal width, anterior margin angulate, lateral mar-



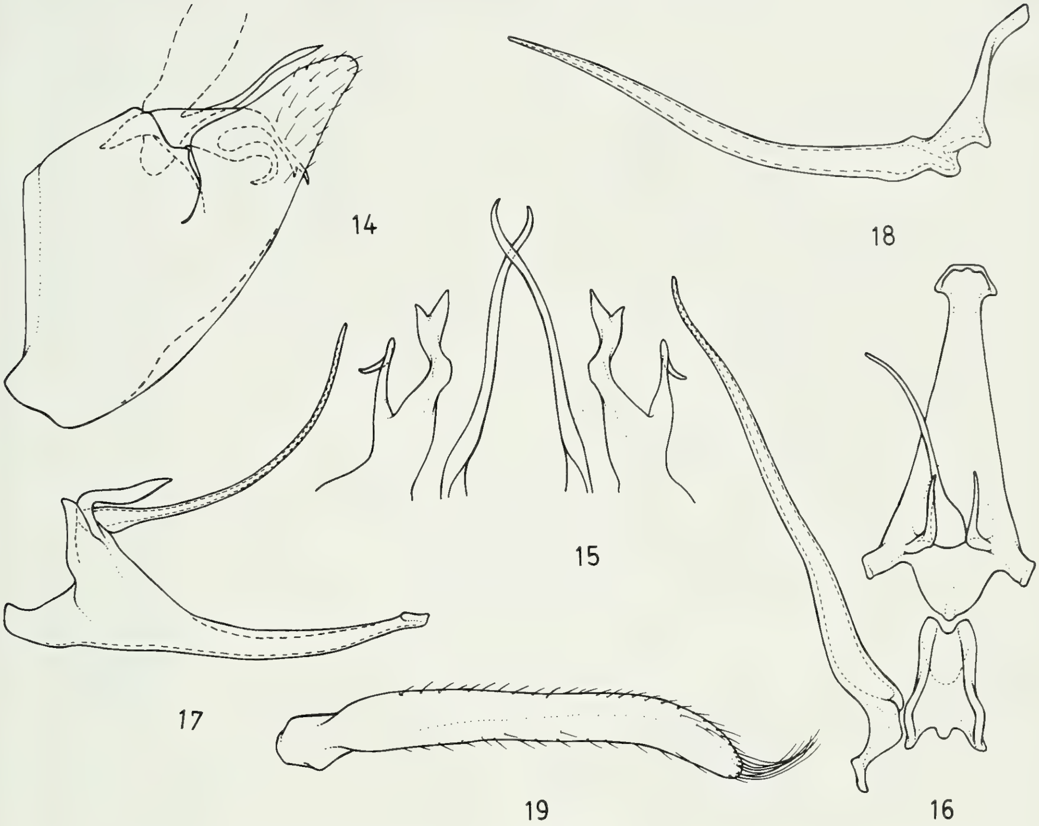
Figs. 7–13. *Thagria melichari*: 7, Head and pronotum, dorsal view. 8, Face, ventral view. 9, Male pygofer and 10th segment, lateral view. 10, Tenth segment and pygofer processes, dorsal view. 11, Aedeagus and ventral paraphysis, dorsal view. 12, Aedeagus and ventral paraphysis, lateral view. 13, Right style, lateral view.

gins convergent basally; eyes large, elongate-ovoid; pronotum large with median longitudinal carina; forewing with venation typical of genus; clypeus long and rather broad; clypellus slightly swollen basally, basal width nearly equal to basal width of clypeus (Fig. 8).

MALE: Pygofer with long, narrow, caudoventral lobe, caudodorsal margin with pair of broad processes (Fig. 9); 10th segment with pair of long ventral processes, processes broad basally, abruptly tapered distally with small projection laterally near middle of process (Figs. 9, 10); aedeagus symmetrical, moderately long, about half as long as ventral paraphysis (Fig. 11); ventral paraphysis slightly asymmetrical, very broad basally in dorsal view, asymmetrically clefted distally, with pair of long basal processes (Figs. 11, 12); style very long, slender, pointed distally and curved laterally in lateral view (Fig. 13); plate long and narrow, typical of genus.

HOLOTYPE (male), THAILAND: Muok-Lek, 1,000 ft, ____. I. ____., H. Fruhstorfer. Additional labels with following information: "H. Fruhstorfer, vend. 25. V. 1924," "*Arya hyalinopunctata* n. sp., manuscript name, L. Melichar det." (MM). Allotype (female), THAILAND: Pakchong, 100 m N of Bangkok, Dec. 2, 1957, J. L. Gressitt (BPBM). Paratypes: VIET NAM: 33 km NE Ban Me Thuot, 500 m, 1 female, 16–18. V. 1960, L. W. Quate (author's collection).

REMARKS: This species is similar in male genitalia characters to *sarawakensis* Nielson but can be separated by the configuration of the 10th segment processes and caudodorsal processes of the pygofer, by the asymmetrically clefted apex of the ventral paraphysis, and by the current geographical range. This species is named for Dr. Leopold Melichar in recognition of his outstanding contributions to leafhopper systematics.



Figs. 14–19. *Thagria insolentis*: 14, Male pygofer and 10th segment, lateral view. 15, Tenth segment and pygofer processes, dorsal view. 16, Connective, aedeagus, ventral paraphysis, and right style, dorsal view. 17, Aedeagus and ventral paraphysis, lateral view. 18, Right style, lateral view. 19, Plate, ventral view.

Thagria insolentis, n. sp.

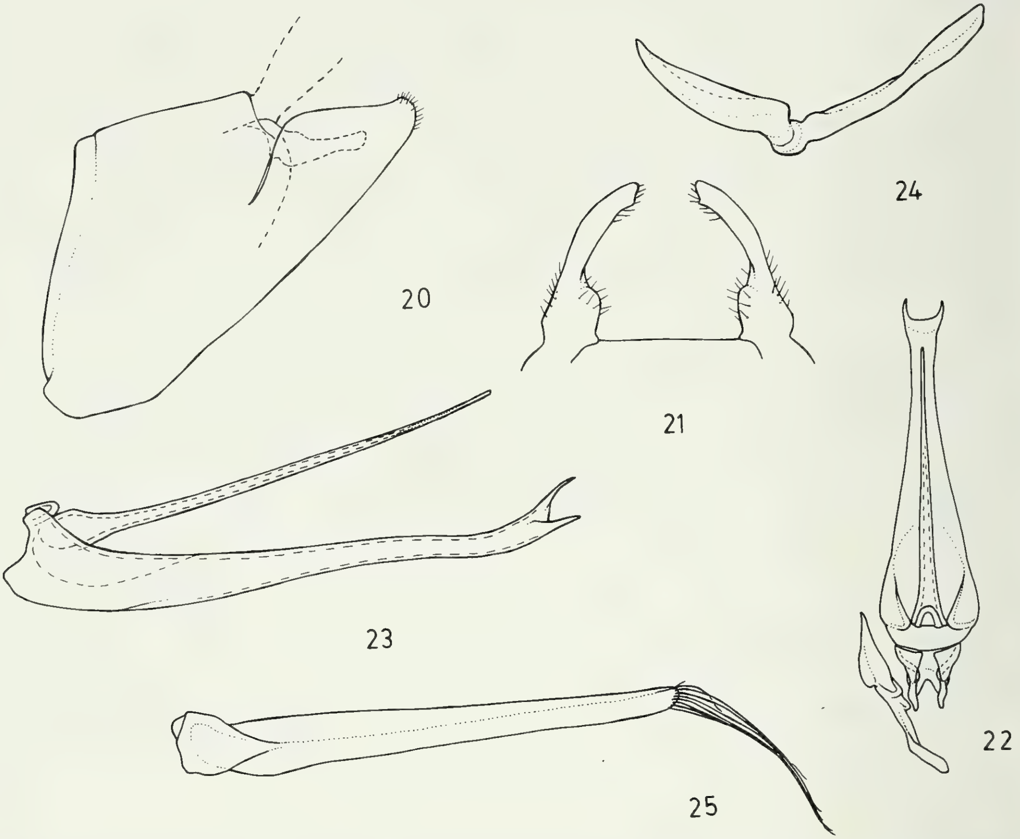
Figs. 14–19

LENGTH: Male 5.90 mm.

Small, slightly robust species. General color light brown with numerous irregular tannish markings on forewings, bullae on dark pronotum ochraceus, crown light tan basally with blackish markings anteriorly, face reddish brown.

Head large, subconical, narrower than pronotum; crown somewhat narrow, width less than transocular width, elevated above level of eyes, produced beyond anterior margin of eyes; eyes large, semiglobular; pronotum short, median length about equal to median length of crown, with short median longitudinal carina originating on anterior margin; scutellum large; forewing moderately long, venation as in description of genus; clypeus long, narrow, excised near antennal sockets; clypellus long and narrow, lateral margins nearly parallel.

MALE: Pygofer in lateral view with elongate triangular caudoventral lobe (Fig. 14); caudodorsal margin with ornate process, process broad basally, abruptly decurved medially with narrow, asymmetrical bifid apex, ventral margin with narrow, hooked secondary process on middle, dorsal margin with short secondary process (Figs. 14, 15); 10th segment with pair of narrow long processes nearly reaching to apex of caudoventral lobe (Fig. 14); aedeagus symmetrical, very long and tubular, curved dorsally at distal half and extending to about apex of ventral paraphysis in lateral view (Figs. 16, 17); ventral paraphysis symmetrical, broad basally with pair of long narrow processes basally on dorsal margin, lateral margins of paraphysis convergent distally to narrow convex apex with short dentate subapical projections laterally (Figs. 16, 17); style very long, attennuated, and sharply pointed api-



Figs. 20–25. *Thagria marissae*: 20, Male pygofer, lateral view. 21, Pygofer processes, dorsal view. 22, Connective, aedeagus, ventral paraphysis, and right style, dorsal view. 23, Aedeagus and ventral paraphysis, lateral view. 24, Right style, lateral view. 25, Plate, ventral view.

cally, exceeding apex of paraphysis (Fig. 16); plate long and narrow, with many long microsetae apically (Fig. 19).

HOLOTYPE (male): [ORIENTAL REGION]: Friese, Teoor (or Tevor), no date, no collector (NM).

REMARKS: The species is near *luteifascia* (Walker). It can be easily distinguished from that species by the ornate caudodorsal processes of the pygofer. The locality of this species is not known but is presumed to be in the Oriental region. In a recent communication from Dr. A. Kaltenbach, Naturhistorishces Museum, Vienna, he stated that the specimen may have come from the Friese collection (H. Freise, 1860–1948) but did not know if Friese collected in the Oriental region.

Thagria marissae, n. sp.

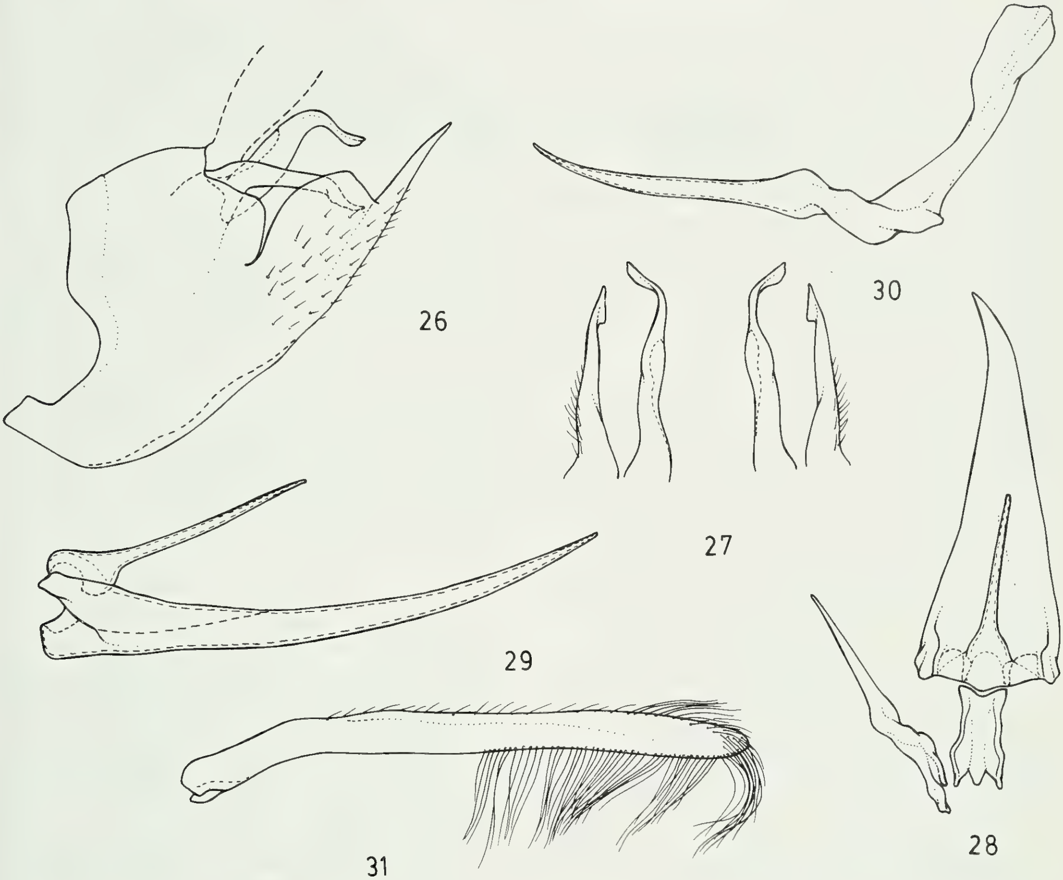
Figs. 20–25

LENGTH: Male 5.75 mm.

Small, slender species. General color light golden brown, suffused with brown markings near apex of forewings and near middle of costa.

Head large, narrower than pronotum, subconical; crown broad, about as wide as eyes, produced distally beyond anterior margin of eyes, lateral margins convergent basally, elevated above level of eyes; eyes large, semiglobular; pronotum and scutellum short, median length of each nearly equal; forewing long and narrow, venation typical of genus; clypeus broad anteriorly, clypellus short, lateral margins nearly parallel.

MALE: Pygofer in lateral view with short broad caudoventral lobe, tapered toward apex, apex rounded, caudodorsal margin with short narrow lobelike process extending distally and not reaching apex of caudoventral lobe (Figs. 20, 21); 10th segment short, simple, without ventral processes (Fig. 20); aedeagus symmetrical, very long and narrow,



Figs. 26–31. *Thagria unidentata*: 26, Male pygofer and 10th segment, lateral view. 27, Tenth segment and pygofer processes, dorsal view. 28, Connective, aedeagus, ventral paraphysis, and right style, dorsal view. 29, Aedeagus and ventral paraphysis, lateral view. 30, Right style, lateral view. 31, Plate, ventral view.

nearly reaching to apex of ventral paraphysis (Figs. 22, 23); ventral paraphysis asymmetrical, broad basally with gradual constriction along middle and slightly expanded distally in dorsal view with pair of short unequal, sharply pointed, lateral processes apically (Figs. 22, 23); style very short, extending just beyond base of aedeagus in dorsal view, narrowly triangular in dorsal view (Fig. 22); plate long and very narrow throughout with tuft of long microsetae apically (Fig. 25).

HOLOTYPE (male): CHINA: Iwa Bi, Hainan Isl., 25. VII. 1935, L. Gressitt (NCSU).

REMARKS: *Thagria marissae* is similar to *T. lurida* (Melichar). It can be separated from *lurida* by the narrower caudoventral lobe of the pygofer, by the longer aedeagus that reaches to the apex of the ventral paraphysis, by the asymmetrical ventral paraphysis, and by its known geographical range. I name this species for my granddaughter, Marissa Jean Hammer.

Thagria unidentata, n. sp.

Figs. 26–31

LENGTH: Male, 7.25–7.75 mm.

Moderately long, slender species. General color tannish brown; eyes tan to brown; crown and pronotum tan, posterior margin of pronotum blackish; scutellum tan to brown; forewing translucent, veins blackish; face tan.

Head much narrower than pronotum, subconical; crown narrower than width of eyes, produced beyond anterior margin of eyes, narrowly rounded distally, lateral margins convergent basally, slightly carinate laterally; pronotum and scutellum equal in length, each equal in length of crown; forewing long and narrow, venation typical of genus; clypeus long and narrow, lateral margins constricted near antennal sockets; clypellus short, lateral margins wider distally than proximally.

MALE: Pygofer in lateral view with short caudoventral lobe, lobe with long spine on caudoventral margin, spine as long as lobe, caudodorsal margin of pygofer with single long process, process sharply pointed apically, curved posterioventrally, and reaching to apex of caudoventral lobe of pygofer (Fig. 26); 10th segment with pair of long processes, processes decurved ventrally at distal 1/3 (Fig. 27); aedeagus short, tubular, reaching to about midlength of ventral paraphysis (Fig. 28); ventral paraphysis slightly asymmetrical in dorsal view, broad basally with lateral margins gradually convergent distally, distal 1/3 slightly undulated with apex slightly curved laterally (Figs. 28, 29); style short, not reaching midlength of ventral paraphysis, distal half narrowly attenuated (Figs. 28, 30); plate long and narrow throughout, with long microsetae on lateral margins and at apex (Fig. 31).

HOLOTYPE (male): INDONESIA: Siberat Isl., West Sumatra, ____.IX. 1924, B. K. and N. Raffles, Singapore Museum (BMNH). Paratypes. 1 male, same data as holotype (author's collection).

REMARKS: *Thagria unidentata* is similar to *T. fryeri* (Distant) but lacks the distinctive lateral processes on the dorsal margin of the ventral paraphysis and has a much longer spine on the caudoventral margin of the caudoventral lobe of the pygofer.

ACKNOWLEDGMENTS

The loan of specimens from the following individuals and their institutions is much appreciated: the late Dr. J. Linsley Gressitt, Bernice P. Bishop Museum, Honolulu (BPBM), Dr. K. G. A. Hamilton, Canada National Collection, Ottawa (CNC), Dr. A. Kaltenbach, Naturhistorische Museum, Vienna (NM), Dr. W. J. Knight, British Museum (Natural History), London (BMNH), Dr. Pavel Lauterer, Moravian Museum, Brno (MM), and Dr. David A. Young (retired), North Carolina State University, Raleigh (NCSU). I thank Jean Stanger for the fine illustrative work and Dr. James P. Kramer, U.S. National Museum, Washington, D.C., and Dr. Paul W. Oman, Oregon State University, Corvallis, for reviewing the paper.

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GENUS *PARALIDIA* WITH DESCRIPTIONS OF NEW SPECIES (HOMOPTERA: CICADELLIDAE: COELIDIINAE)

M. W. Nielson[1]

ABSTRACT.—The generic concept of *Paralidia* Nielson, type-species, *Coelidia plaumanni* Linnavuori, is reelucidated after five additional new species were found in South America. These are described and illustrated. Four species, all from Brazil, include *spinata, retrorsa, denticulata,* and *bispinosa*. One species, *singularis*, is from Ecuador. A key to males of the six known species is also presented.

The monobasic genus *Paralidia* was established for *Coelidia plaumanni* Linnavuori in the tribe Coelidiini by Nielson (1982). Since its erection five additional species have been found. These not only broaden the concept of the genus but also solidify its taxonomic and zoological base.

Generic characterization, in addition to that previously described, includes the following features: Small to moderately large, slender species; head slightly to distinctly narrower than pronotum; crown always narrow and produced slightly to nearly 1/3 of its median length beyond anterior margin of crown, lateral margins parallel to convergent basally and varying from slightly to prominently carinate; pronotum and scutellum usually short and nearly always equal to or shorter than crown; clypeus nearly always narrower anteriorly than basally; male pygofer with caudoventral process always present, slender and long, but varying in length, degree of fusion basally with caudal margin of pygofer and configuration; aedeagus nearly always asymmetrical, usually narrow and somewhat tubular, always with dorsally curved apex that usually has 1-3 spines, sometimes with serrations or spines on middle of shaft; style varies from moderately long to very long (reaching apex of aedeagus) and very slender at distal 2/3, sometimes enlarged preapically; plate long with middle third of outer margin enlarged and convex, always profusely setose with long microsetae.

The known species occur in the eastern states of Brazil, with one species from Ecuador. The host plants, biology, and economic importance of the group are not known. Females are rarely collected.

Key to Males of *Paralidia*

1. Aedeagus with 1-3 spines on or near apex, spines along middle of shaft absent 2

— Aedeagus without apical spines; spines along middle of shaft present (Fig. 4). . . .*spinata*, n. sp.

2(1). Aedeagus with 2–3 spines on or near apex 3

— Aedeagus with a single terminal spine (Fig. 13) .... *singularis* n. sp.

3(2). Aedeagus with 2 apical or subapical spines 4

— Aedeagus with 1 apical and 2 subapical spines (Fig. 19) .... *retrorsa*, n. sp.

4(3). Aedeagus with 2 subapical, needlelike spines, spines asymmetrical and not originating on the same sagittal plane......................... 5

— Aedeagus with 2 apical, basally broad spines, spines symmetrical and originating on the same sagittal plane (Fig. 799[2], Nielson 1982) .... *plaumanni* (Linnavuori)

5(4). Aedeagus with dentate, lateral flange on one side of middle of shaft; pygofer with a partially fused, membranous caudoventral process; style needlelike at distal 2/3 (Fig. 28) .... *denticulata*, n. sp.

— Aedeagus without such flange; pygofer with well-developed caudoventral process; style with a preapical expansion (Fig. 35)......... .... *bispinosa*, n. sp.

Paralidia spinata n. sp.

Figs. 1–8

LENGTH: Male 6.15–6.80 mm, female 7.70 mm.

Moderate-sized, slender species. General color pale ochre with broad (narrow in fe-

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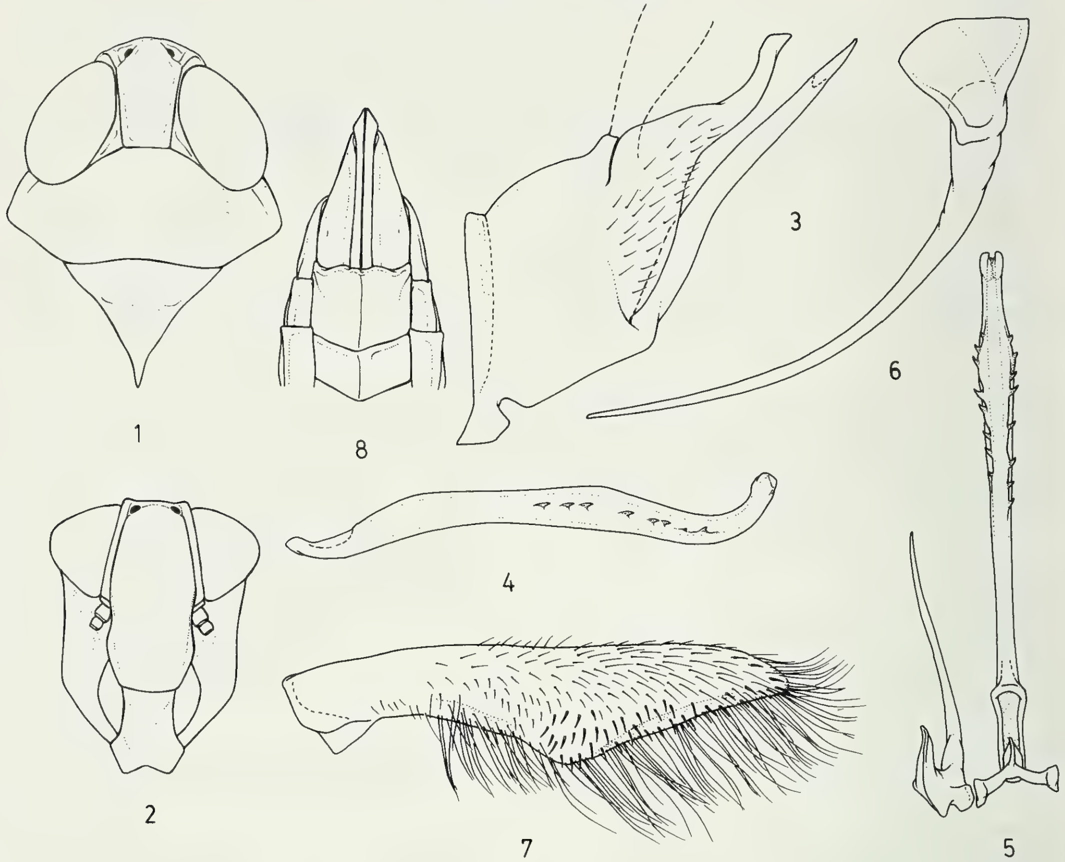
[1] Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah 84602.

[2] Separation of apical spines not apparent in Figure 799.



Figs. 1–8. *Paralidia spinata*: 1, Head, pronotum and scutellum, dorsal view; 2, Face, ventral view; 3, Male pygofer, lateral view; 4, Aedeagus, lateral view; 5, Connective, aedeagus and right style, dorsal view; 6, Style, lateral view; 7, Plate, ventral view; 8, Female abdominal venter, ventral view.

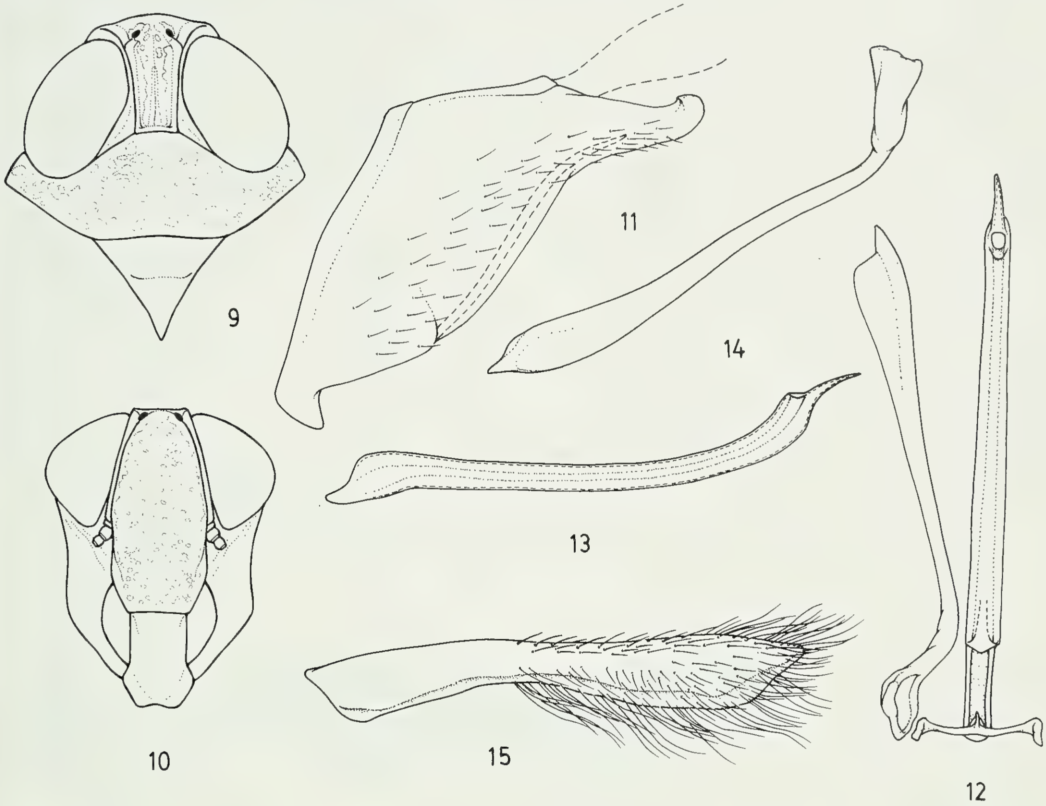
male), black, medial longitudinal band from crown to near forewing apex, eyes light reddish brown, face ochre.

Head rather large, narrower than pronotum (Fig. 1); crown very narrow, produced slightly beyond anterior margin of eyes, rounded distally, lateral margins carinate and parallel; eyes very large, about twice as wide as coronal width, semiglobular; pronotum and scutellum short, median length of each slightly less than median length of crown; forewing elongate, venation typical of genus; clypeus long and broad, lateral margins broadly convex; clypellus short, lateral margins broader distally (Fig. 2).

MALE: Pygofer in lateral view with a long, narrow slightly sinuate, acuminate caudoventral process, process broad at basal 1/3, caudodorsal margin with a shorter, narrow sinuate process, apex curved slightly downward and bluntly pointed (Fig. 3); aedeagus symmetrical, long, nearly tubular throughout, slightly compressed laterally with numerous conspicuous dentate microspines laterally on distal half of shaft before apex, spines not as readily apparent in some specimens, apex curved dorsally in lateral view, rounded apically and without terminal spines (Figs. 4, 5); gonopore terminal; connective as in *singularis*; style long, reaching to about midlength of aedeagal shaft, needlelike at distal half (Figs. 5, 6); plate long, similar in shape to *singularis* except apex more pointed, profusely setose (microsetae) (Fig. 7).

FEMALE: Seventh sternum nearly twice as long as preceding segment, caudal margin sinuate (Fig. 8).

HOLOTYPE (male): BRAZIL: Minaes Gerais, Santa Barabara, Caraca, ____.I. 1970, F. M. Oliveira, B. M. 1971–165 (BMNH). Allotype



Figs. 9–15. *Paralidia singularis*: 9, Head, pronotum and scutellum, dorsal view; 10, Face, ventral view; 11, Male pygofer, lateral view; 12, Connective, aedeagus and right style, dorsal view; 13, Aedeagus, lateral view; 14, Style, lateral view; 15, Plate, ventral view.

(female), Minaes Gerais, Delfim Moreira, 1,100 m, ____.II.1972, F. M. Oliveira, B. M. 1972–541 (BMNH). Paratypes: 4 males, same data as holotype, 4 males, same data as allotype (BMNH), 2 males, same data as holotype (USNM, author's collection).

REMARKS: *Paralidia spinata* is similar to *denticulata* but can be separated from it and all other species in the genus by the minute spines on the aedeagal shaft, which also lacks terminal spine(s).

Paralidia singularis, n. sp.

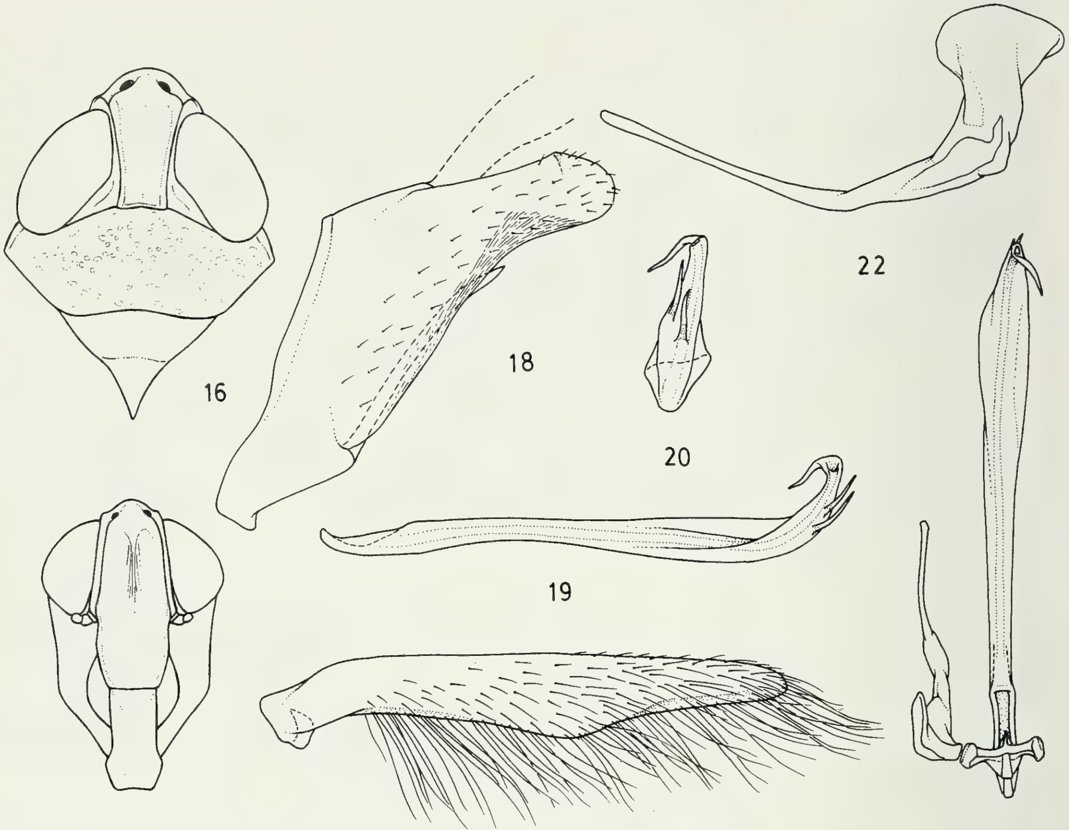
Figs. 9–15

LENGTH: Male 5.50 mm.

Small, slender species. General color dark brown with large, triangular, pale translucent spot on middle of forewing and with numerous pale spots on veins; eyes deep reddish brown; pronotum with small pale spots; clypeus and clypellus black with small pale spots.

Head large, narrower than pronotum (Fig. 9); crown very narrow, produced slightly beyond anterior margin of eyes, rounded distally, lateral margins carinate; eyes very large, more than twice as wide as basal width of crown, semiglobular; pronotum and scutellum short; elytra long and moderately broad; clypeus long and narrow, narrower anteriorly than basally; clypellus short, narrow, lateral margins broad distally (Fig. 10).

MALE: Pygofer in lateral view with very long, slender, caudoventral process reaching nearly to apex of caudodorsal process, caudodorsal process moderately long, lobelike, apex curved dorsally (Fig. 11); aedeagus symmetrical or nearly so, long, nearly tubular throughout with single prominent, sharply pointed spine apically (Fig. 12), apex of shaft curved dorsally with spine projecting caudodorsally (Fig. 13); gonopore apical near base of spine; connective stout, Y-shaped,



Figs. 16–23. *Paralidia retrorsa*: 16, Head, pronotum and scutellum, dorsal view; 17, Face, ventral view; 18, Male pygofer, lateral view; 19, Aedeagus, lateral view; 20, Terminus of aedeagal shaft, caudal view; 21, Connective, aedeagus and right style, dorsal view; 22, Style, lateral view; 23, Plate, ventral view.

with short stem; style very long and slender, nearly reaching apex of aedeagus, distal third expanded except for abruptly pointed apex (Fig. 12, 14); plate long, narrowed subbasally, broad subapically and abruptly narrowed to a bluntly rounded apex, with numerous long microsetae (Fig. 15).

HOLOTYPE (male): ECUADOR: Quito (Equateur), ____.X.1930, R. Benoist (MNHN).

REMARKS: *Paralidia singularis* is nearest to *retrorsa* n. sp. and can be distinguished by the single long spine on the apex of the aedeagus and by the large pale triangular spot on the middle of the forewing.

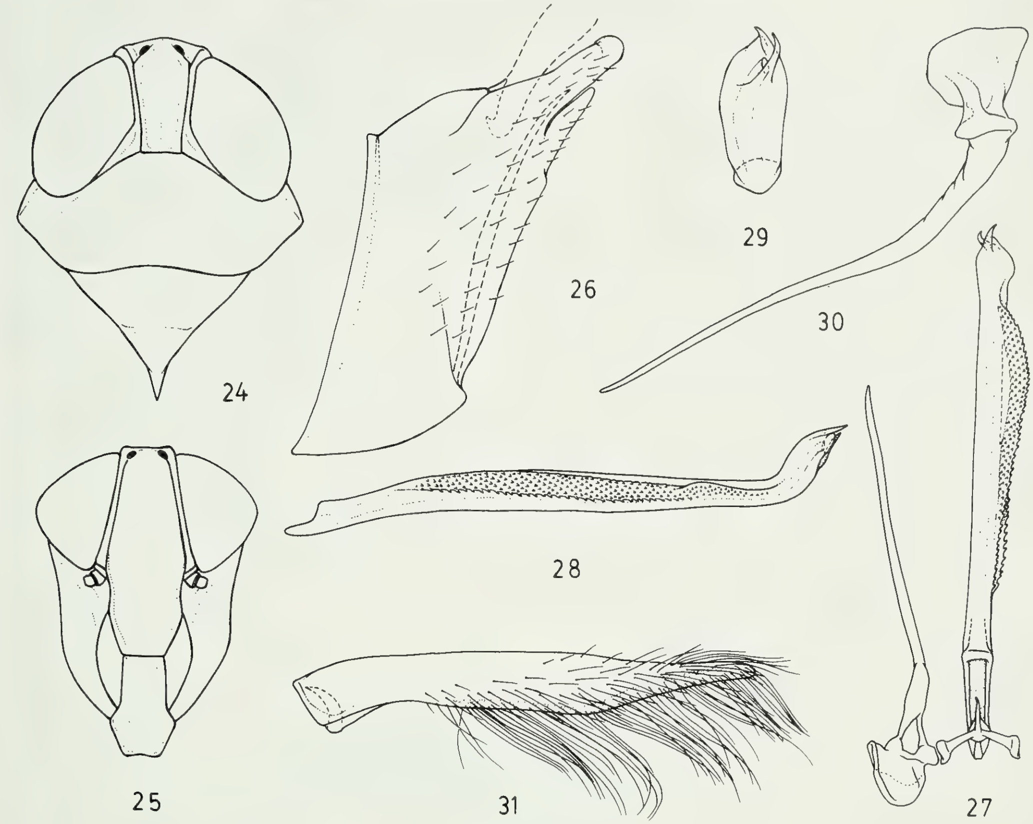
Paralidia retrorsa, n. sp.

Figs. 16–23

LENGTH: Male 6.90 mm, female 7.25–8.00 mm.

Moderate-sized, slender species. General color dark brown to black except for pale face, crown and costa of forewing deep tan, veins of forewing sometimes mottled.

Head large, narrower than pronotum (Fig. 16); crown very narrow, about 1/2 width of eyes, much produced distally beyond anterior margin of eyes, distal length nearly 1/3 entire median length, anterior margin acutely rounded, disk foveate medially, lateral margins nearly parallel, slightly carinate; eyes very large, elongate-ovoid; pronotum and crown short, each shorter than median length of crown; forewing elongate, venation typical of genus; clypeus long and narrow, narrower anteriorly than posteriorly with short broad ridge medially and originating on anterior margin then dividing into several rugose lines that terminate about middle; clypellus long and narrow, lateral margins expanding distally (Fig. 17).



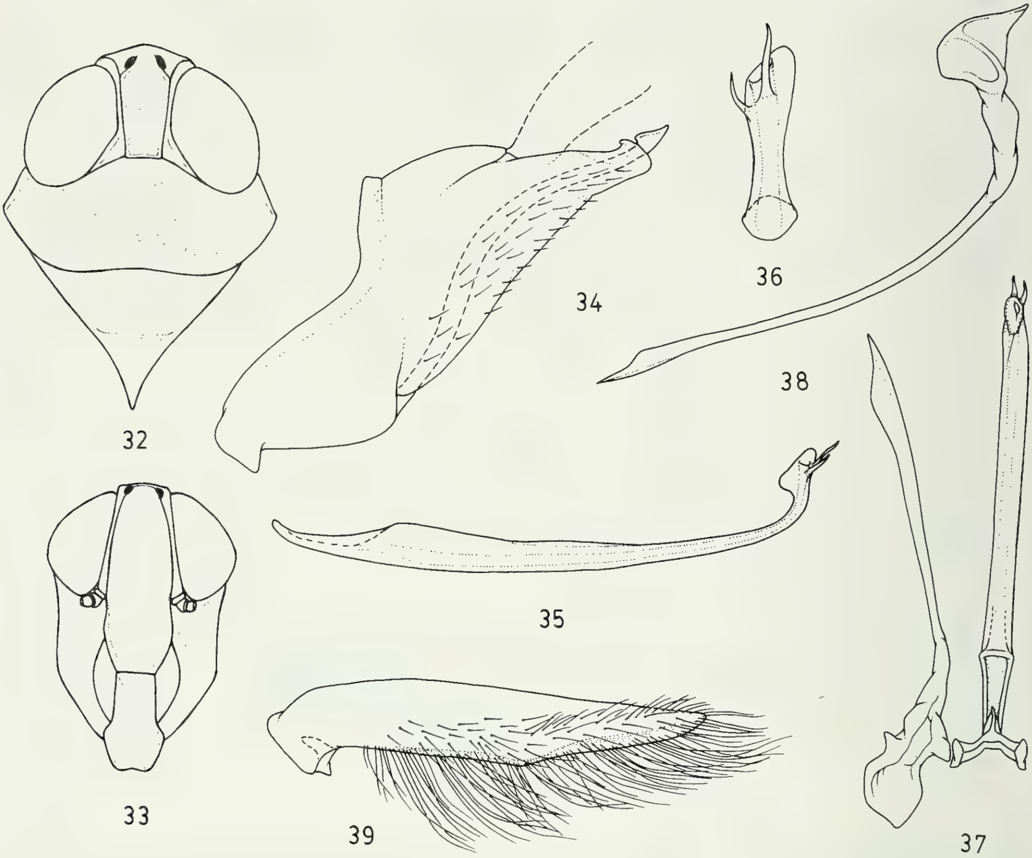
Figs. 24–31. *Paralidia denticulata*: 24, Head, pronotum and scutellum, dorsal view; 25, Face, ventral view; 26, Male pygofer, lateral view; 27, Connective, right style and aedeagus, dorsal view; 28, Aedeagus, lateral view; 29, Terminus of aedeagal shaft, caudal view; 30, Style, lateral view; 31, Plate, ventral view.

MALE: Pygofer in lateral view with weakly sclerotized caudoventral process, process similar to *denticulata* but fused to pygofer at more than half its base, caudodorsal margin with short, broad lobe, lobe rounded apically with short, bluntly pointed process subapically on dorsal margin, process directed mesally (Fig. 18); aedeagus asymmetrical, very long and narrow, apex abruptly curved dorsally in lateral view and terminating with single curved, sharply pointed, retrorse spine (Fig. 19), two additional membranous spines on caudal margin of curved apex, one above the other, not on same sagittal line and both pointed dorsally (Fig. 20), dorsolateral margins of shaft basad of apex not parallel at distal 1/3 in lateral view (Fig. 19); gonopore apical near base of terminal spine; connective as in genus; style moderately long, distal half very narrow and membranous (Figs. 21, 22); plate long and narrow, similar in configuration to *P. plaummani* (Linnavuori) with numerous long microsetae (Fig. 23).

FEMALE: Seventh sternum about twice as long as preceding segment, caudal margin sinuate as in *spinata*.

HOLOTYPE (male): BRAZIL: no locality, no date, M. Alvarenga, B.M. 1971–165 (BMNH). Allotype (female), same data as holotype (BMNH). Paratypes: 3 females, same data as holotype (BMNH), 1 female, Sao Paulo, S. Barreiro, S. Bocaina, 1,650 m, ____.XII.1968, M. Alvarenga, B.M. 1970–484 (author's collection).

REMARKS: This species is similar in general habitus and male genital characters to *spinata* n. sp. but can be distinguished by the short, anterior median clypeal ridge, by the prominent asymmetrical aedeagus, and by the retrorse terminal spine with 2 subterminal attendant spines on the aedeagus. The well-produced crown will also separate this species from all others in the genus.



Figs. 32–39. *Paralidia bispinosa*: 32, Head, pronotum and scutellum, dorsal view; 33, Face, ventral view; 34, Male pygofer, lateral view; 35, Aedeagus, lateral view; 36, Terminus of aedeagal shaft, caudal view; 37, Connective, right style and aedeagus, dorsal view; 38, Style, lateral view; 39, Plate, ventral view.

Paralidia denticulata, n. sp.

Figs. 24–31

LENGTH: Male 6.90–7.10 mm.

Medium-sized, slender species. General color light reddish brown with suffused deep brown medially on distal half of forewings, face tannish brown.

Head moderately large, subconical, narrower than pronotum (Fig. 24); crown very narrow, produced distally beyond anterior margin of eyes, narrowly rounded distally, lateral margins broadly convex, carinate; eyes very large, elongate-ovoid; pronotum long, median length slightly greater than median length of crown; scutellum small; forewing elongate, venation typical of genus; clypeus long and narrow, narrower anteriorly than basally; clypellus long and narrow (Fig. 25).

MALE: Pygofer in lateral view with long, very narrow, acuminate caudoventral process, process completely hidden by caudal margin of pygofer, caudodorsal margin with short truncate lobe (Fig. 26); aedeagus asymmetrical, long, subtubular throughout with lateral finely dentate asymmetrical flange along middle of dorsal margin in dorsal view (Fig. 27) and rows of fine teeth below on middle 2/3 of shaft, apex of shaft abruptly curved dorsally in lateral view with 2 very short, sharp spines apically, one below the other but not originating on the same sagittal line (Figs. 28, 29); gonopore apical between spines; connective typical of genus; style long, extending beyond midlength of aedeagal shaft, needlelike at apical 2/3 (Fig. 30); plate typical of genus, profusely setose (Fig. 31).

HOLOTYPE (male): BRAZIL: Rio de Janeiro, Guanabara, ____.X.1970, M. Alvarenga, B.M. 1971–165 (BMNH). Paratypes: BRAZIL: Bahia, Itapetinga, ____.IX. 1969.

F. M. Oliveira, B. M. 1971–165 (author's collection).

REMARKS: *Paralidia denticulata* is similar to *spinata* n. sp. but can be separated from it by the lateral tooth flange that occupies the greater middle of the aedeagal shaft and by the presence of apical spines.

Paralidia bispinosa, n. sp.

Figs. 32–39

LENGTH: Male 8.10 mm.

Large, slender species. General color tannish throughout, pale spots on dark veins of forewings.

Head large, distinctly narrower than pronotum (Fig. 32); crown very narrow, about 1/2 as wide as transocular width, produced beyond anterior margin of eyes, anterior margin angled, lateral margins slightly convergent basally, carinate; eyes very large, semiglobular; pronotum and scutellum short, each with median length about equal to length of crown; forewings elongate, venation typical of genus; clypeus long and narrow, narrower anteriorly than posteriorly; clypellus long and narrow, lateral margins broad distally (Fig. 33).

MALE: Pygofer in lateral view with long, narrow, heavily sclerotized, broadly curved caudoventral process, process extending beyond caudodorsal lobe and subtriangulate distally, caudodorsal margin with broad, moderately long lobe, apex dentate dorsally (Fig. 34); aedeagus asymmetrical, long, tubular, with apex curved dorsally in lateral view (Fig. 35), 2 membranous spines on caudal margin of curved apex, spines unequal in length, one below the other and not originating on the same median sagittal line (Fig. 36); gonopore terminal; style very long, nearly reaching apex of aedeagus, narrow except for base and expansion subapically (Figs. 37, 38); plate long, configuration very similar to other species in the genus, profusely setose (microsetae) (Fig. 39).

HOLOTYPE (male): BRAZIL. Sao Paulo, Salesopolis county, Estaceo Biologica de Boracela. Cloud Forest, 850 m, 23.II.1969, W. J. Knight. B.M. 1970–484 (BMNH).

REMARKS: *P. bispinosa* is the largest known species. It is similar in aedeagal characters to *denticulata*, but it is larger, lacks the serrate flange, and has a well-developed caudoventral process on the pygofer.

ACKNOWLEDGMENTS

The material described herein was kindly furnished by the generosity of Dr. W. J. Knight, British Museum (Natural History) (BMNH), and Dr. Michel Boulard, Museum National d'Histoire Naturelle, Paris. I thank Jean Stanger for her fine illustrations and Dr. James P. Kramer, U.S. National Museum, Washington, and Dr. Paul W. Oman, Oregon State University, Corvallis, for reviewing the manuscript.

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MONTANE INSULAR BUTTERFLY BIOGEOGRAPHY: FAUNA OF BALL MOUNTAIN, SISKIYOU COUNTY, CALIFORNIA

Arthur M. Shapiro[1]

ABSTRACT.—Ball Mountain is an isolated, mostly heavily forested peak reaching the subalpine zone (2,330 m) in eastern Siskiyou County north of Mt. Shasta, California. It supports a rich fauna of at least 68 butterfly species showing affinities to the faunas of the Trinity Alps and Eddies, the Warners, and the Cascades. Rare or endemic entities include *Speyeria mormonia*, *Lycaena heteronea gravenotata*, and melanic forms of *Speyeria atlantis* and *Agriades "glandon."* Several zones of intergradation or hybridization impinge on the fauna as well.

Both the physical and biotic geography of northern California are very complex. The jumbled terrain of the Klamath-Trinity-Siskiyou upland and the volcanic southern Cascades provides rapid climatic gradients that are reflected in the plant communities of the region. Most of these communities are still inadequately characterized, and several important areas are poorly known even from a floristic standpoint. The butterfly faunas of northern California were extremely poorly documented prior to the 1970s, with only one major paper (Williams 1909) and scattered specimens in museums, often inadequately labeled. From 1976 through 1980 a major effort was mounted to document the butterfly fauna of the Trinity Alps and the Eddies (Shapiro, Palm, and Wcislo 1981) in the hope of using these faunas to test some historical scenarios advanced by botanists to account for the origins of the subalpine and alpine biota of the Sierra Nevada range. Although no definitive tests of those scenarios emerged, this study uncovered so much unanticipated complexity (along with anticipated Klamath endemism) in the Trinity-Eddy faunas that it has been continued at several sites which, by virtue of unique location, topography, or vegetation seemed most likely to provide important information on the biogeographic history of the northern California butterfly faunas. An especially rewarding site is Ball Mountain, Siskiyou County.

Ball Mountain is one of only three peaks between Mount Shasta and the Oregon border, east of U.S. Highway 5, to reach above 2,270 m. The highest of them, Goosenest, at 2,812 m, is a recent Cascade volcano with a poorly vegetated lava cone, though it does have some rare alpine plants (e.g., *Hulsea nana* Gray, Compositae, which it shares with two other recent volcanoes, Mts. Lassen and Shasta, and with the nonvolcanic Mt. Eddy). The other two, Willow Creek Mountain (2,676 m) and Ball Mountain, (2,330 m), are only 8 km apart and share a common base and access by road. Both are older, Pliocene volcanoes, mostly basaltic (Ball) or andesitic (Willow Creek). Ball Mountain has two old vents marked by pyroclastic jumbles; the higher of these bears a fire watchtower. There is no evidence of recent (Holocene) volcanic impact on the vegetation of the mountain, which has presumably evolved to its present state through the Pleistocene and thereafter. Ball Mountain and Willow Creek Mountain rise fairly gradually from a rolling volcanic upland, the Little Shasta country, to the west (largely Tertiary flows, with altitudes from 750–1,200 m); Ball Mountain, the more easterly, drops off abruptly to the Quaternary lake-bed alluvial plain near Macdoel, ca 1,275 m (Fig. 1).

Although Willow Creek Mountain is the higher of the two, it is more continuously forested and has a smaller variety of habitats and less access by road than Ball Mountain. Access to both is provided by USFS road 47NO3, the extension of York Road, which near Lodgepole Station turns northeastward, whereas road 46N11 goes due south to Willow Creek Mountain and 46N10 goes along the flank of Ball Mountain, looping around Little

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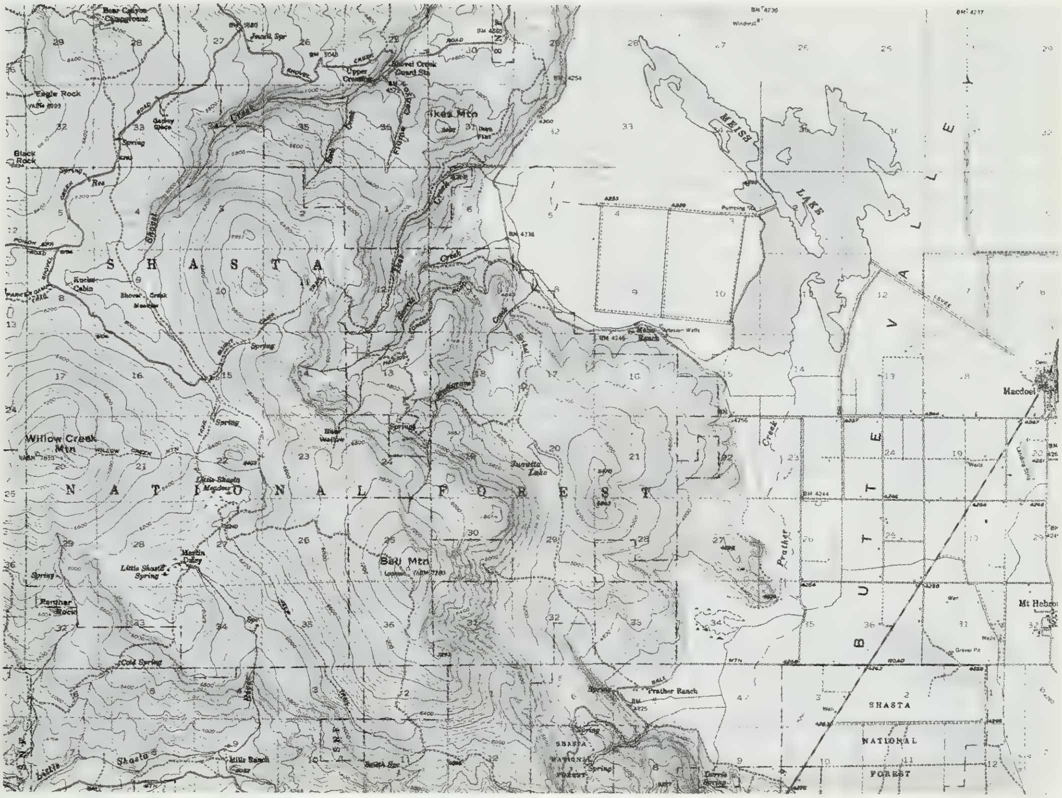
Bear Canyon Campground
Eagle Rock
Black Rock
Upper Creek
Ikes Mtn
MEISS LAKE
SHASTA
NATIONAL FOREST
Willow Creek Mtn
Little Shasta Meadow
Martin Dairy
Little Shasta Spring
Panther Rock
Cold Spring
Bear Wallow
Juanita Lake
Ball Mtn
Prather Creek
Prather Ranch
Mills Ranch
BUTTE VALLEY
Macdoel
Mt Hebron
SHASTA
NATIONAL
FOREST

Fig. 1. Detail of Ball Mountain area from USGS 15′ topographic series, Macdoel quadrangle, 1954. Contour interval 40 feet (12.1 m).

Shasta Meadow and Martin Dairy Campground as 46N09; another spur leads to the lookout. Access for hikers and heavy-duty vehicles is also possible from Ball Mountain Road (unnumbered), which is paved beyond Table Rock (1,130 m) but becomes nearly impassable to most vehicles thereafter. This road joins the USFS roads south of Martin Dairy. The entire area is mapped on the USFS map of the Klamath National Forest, Goosenest Ranger District. The best detail is on the 1968 version. The Ball Mountain lookout is R6.E, T45.N. The entire area reported on in this paper can be collected comfortably by two people in one day, or by one person in two days, with a vehicle.

VEGETATION

The vegetation of Ball Mountain is apparently undescribed in the botanical or forestry literature. Like many mountains in northern California, it provides a "telescoped" sequence of Merriam's "Life Zones," such that one may drive from "Upper Sonoran" to "Subalpine" in less than 20 km (this very short linear distance facilitates altitudinal migration of valley and foothill butterflies to the high montane meadows).

The general zonation of forest vegetation on Ball Mountain and the platform on which it sits more or less corresponds to the outline provided by Rundel, Parsons, and Gordon (1977) for the California portion of the Cascades. The lowest elevations, representing an extension of the Little Shasta country, have an open woodland dominated by shrubby forms of Oregon Oak (*Quercus garryana* Dougl.), with juniper (*Juniperus occidentalis* ssp. *occidentalis* Hook., near its southwestern limit) as an associate. This is quickly replaced by a mixed conifer association beginning at just over 900 m, dominated by yellow pine (*Pinus ponderosa* Laws.), with incense cedar (*Calo-*

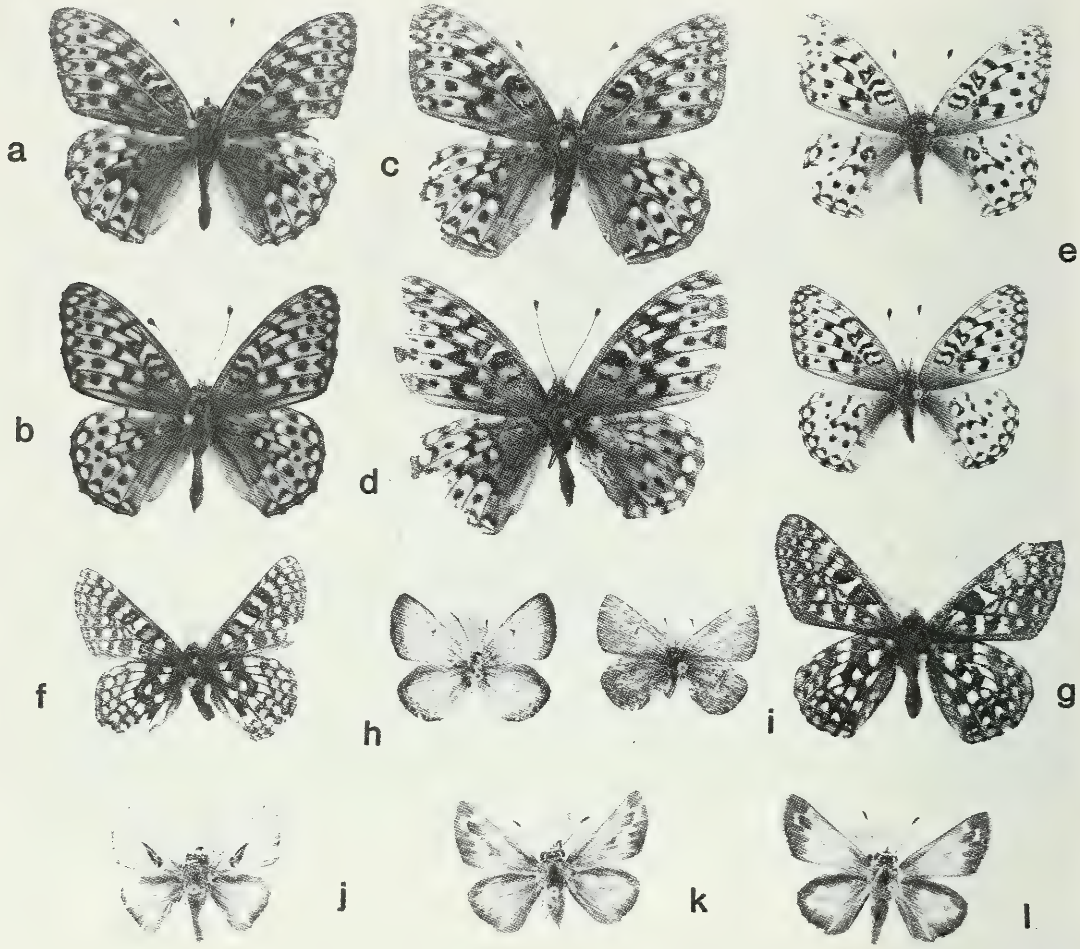

Fig. 2. Rare butterflies from Ball Mountain, dorsal surfaces: a, *Speyeria atlantis* (melanic form), male, viii.10.83; b, same (normal form), male, vii.3.85; c, same (melanic form), female, viii.10.83; d, same (melanic form), female aberration, ix.5.85; e, *Speyeria mormonia*, 2 females, ix.5.85; f, *Euphydryas editha*, male, vi.12.85; g, *Euphydryas chalcedona*, male, vi.12.85; h, *Agriades "glandon,"* male, vii.3.85; i, same, female, vii.3.85; j, *Hesperia harpalus*, male, ix.5.85; k, same, light female, ix.5.85; 1, same, dark female, ix.5.85.

cedrus decurrens Torr.) and white fir (*Abies concolor* Lindl.) locally abundant. At about 1,450 m lodgepole pine (*Pinus contorta* ssp. *murrayana* Grev. & Balf.) first appears in cold and poor sites and quickly becomes dominant; above 1,650 m it is joined by Red Fir (*Abies magnifica* var. *shastensis* Lemm.) and western white pine (*Pinus monticola* Dougl.), and this association continues nearly to the summit. Within it are extensive sedgy and grassy meadows ranging from dry to wet and rimmed by quaking aspen (*Populus tremuloides* Michx.), many of which are uncharacteristically large for the species. These are among the most diverse sites for both herbs and butterflies. The area surrounding both summits supports a virtually pure stand of whitebark pine (*Pinus albicaulis* Engelm.). This subalpine forest is characteristically open, with many herbs and shrubs in the understory; the shrubs, which include sagebrush (*Artemisia tridentata* Nutt.) and *Haplopappus bloomeri* Gray, predominate among the pyroclasts, whereas herbaceous perennials (*Monardella odoratissima* ssp. *pallida* Epl., *Eriogonum umbellatum* Torr., etc.) cover the light, sandy soils elsewhere.

Understory vegetation in the montane conifer forests is extremely undiverse, with extensive areas dominated by pine-mat manzanita (*Arctostaphylos nevadensis* Gray) in successional sites. The greatest herbaceous

TABLE 1. Occurrence of species on Ball Mountain on collecting dates, 1983 and 1985.

	vi.12.85	vii.3.85	vii.15.83	viii.10.83	viii.10.85	ix.5.85	ix.7.83
Papilio zelicaon Lucas	x	x			x		
Papilio rutulus Lucas	x	x					
Papilio eurymedon Lucas		x					
Parnassius clodius Men. ssp.	x	x					
Neophasia menapia Feld. & Feld.					x	x	x
Pontia beckerii Edw.			x		x	x	
Pontia occidentalis Reak.	x	x	x	x	x	x	x
Pieris napi L. ssp.	x						
Pieris rapae L.	x				x	x	
Colias eurytheme Bdv.	x	x	x	x	x	x	x
Colias philodice eriphyle Edw.	x	x	x	x	x	x	
Colias eurytheme X *philodice*	x	x	x	x	x	x	
Anthocharis sara sara Lucas	x						
Euchloe ausonides Lucas	x	x					
Coenonympha "tullia" eryngii H.Edw.			x	x		x	x
Danaus plexippus L.					x	x	
Limenitis lorquini Edw.	x	x	x	x	x		
Adelpha bredowii californica Butl.					x	x	
Vanessa virginiensis Dru.		x	x		x	x	
Vanessa cardui L.			x	x	x		
Vanessa annabella Field		x		x		x	x
Precis coenia Hbn.					x	x	
Nymphalis californica Bdv.	x				x	x	
Nymphalis milberti furcillata Say				x		x	
Nymphalis antiopa L.	x	x				x	
Polygonia faunus rusticus Edw.						x	
Polygonia zephyrus Edw.	x			x		x	x
Phyciodes campestris Behr	x						
Phyciodes mylitta Edw.	x	x	x		x	x	x
Chlosyne hoffmanni segregata B. & McD.		x					
Euphydryas chalcedona nr. *wallacensis* Gund.	x						
Euphydryas editha nr. *edithana* Strand	x						
Boloria epithore Edw.	x	x	x	x			
Speyeria coronis Behr (*snyderi-simaethis* blend zone population)		x				x	
Speyeria zerene conchyliatus Comst.		x	x	x	x	x	x
Speyeria callippe nr. *rupestris* Behr		x	x				
Speyeria egleis nr. *oweni* Edw.	x	x	x	x	x	x	x
Speyeria atlantis Edw. (*dodgei*-melanic endemic)	x	x	x	x	x	x	x
Speyeria mormonia Bdv. ssp.						x	
Speyeria hydaspe purpurascens H.Edw.		x	x	x	x	x	
Satyrium saepium Bdv.				x			
Mitoura nelsoni Bdv.	x						
Mitoura spinetorum Hew.							x
Incisalia fotis nr. *mossii* H.Edw.	x						
Incisalia eryphon Bdv.	x	x					
Lycaena arota Bdv.						x	x
Lycaena heteronea gravenotata Klots				x	x		
Lycaena xanthoides Bdv. - *editha* Mead intergrades			x				
Lycaena gorgon Bdv.			x				
Lycaena hellodies Bdv.	x			x	x	x	x
Lycaena nivalis Bdv. ssp.		x	x	x	x		x
Plebeius "idas" ricei Cross-*anna* Edw. intergrades		x		x	x		
Plebeius saepiolus Bdv.	x	x	x	x			
Plebeius icarioides Bdv. ssp.	x	x		x			
Plebeius acmon Westw. & Hew.		x				x	x
Plebeius lupini Bdv.	x		x				
Agriades "glandon Prun." ssp.		x	x				
Everes amyntula Bdv.	x	x	x				
Glaucopsyche piasus Bdv.	x						
Glaucopsyche lygdamus nr. *columbia* Skin.		x	x				

Table 1 continued.

	vi.12.85	vii.3.85	vii.15.83	viii.10.83	viii.10.85	ix.5.85	ix.7.83
Celastrina argiolus echo Edw.	x						
Ochlodes sylvanoides Bdv.			x	x	x	x	x
Polites sonora Scud.	x	x	x	x			
Hesperia "comma complex"				x	x	x	
Hesperia juba Scud.	x					x	x
Pyrgus ruralis Bdv.	x						
Pyrgus communis Grote						x	
Erynnis icelus Scud. & Burg.	x						
Erynnis propertius Scud. & Burg.	x	x	x	x		x	
Total species recorded[1]	36	32	26	25	25	32	17

[1] Not counting *Colias* hybrids as a species.

diversity seen is at Little Shasta Meadow, which has a great variety of Composites and other showy flowering species. It has a light, sandy soil and supports many of the species also found at the summit in the subalpine forest. There are no true bogs, but the wetter meadows are filled with sedge peat. California pitcher plant (*Darlingtonia californica* Torr.), which is characteristic of boggy meadows in the ultrabasic Trinities and Eddies, is absent. Because the meadows are grazed seasonally by livestock, some herbaceous species may have been lost. Most of the meadows do not display severe sequelae of overgrazing, however.

Important nectar sources for collecting occur primarily along the roads and on the meadows. They are very spotty, resulting in high concentrations of butterflies in very small areas. On 5 September 1985, for example, over 30 species (several hundred individuals) were seen in a walk from Martin Dairy Campground to Kuck's Cabin, but it was common to see nothing but *Speyeria zerene* in 1-km stretches where no flowers were available. Among the most important nectar sources are *Monardella odoratissima*, *Haplopappus bloomeri*, *Eriogonum* spp., *Cirsium vulgare* (Savi)Ten., *Aster* spp., and *Chrysothamnus* spp.

FAUNISTICS AND PHENOLOGY

Table 1 presents a complete itemization of species seen on each of the three days in 1983 and four in 1985, when the mountain was collected thoroughly. Spring was late and cold in 1983, with very heavy and persistent snow pack. Spring was very early, warm, and dry in 1985, with snow completely gone by early June. The early summer was hot and dry and the late summer and autumn cold and wet, culminating in heavy snow to the 1,500 m level on 8 September. The two years of study thus embrace very different conditions and probably reflect accurately the amount of phenological variation to be expected in the Ball Mountain fauna. Most of the fauna is univoltine. The only species definitely having at least two broods are *Pontia occidentalis*, *Phyciodes mylitta*, and *Lycaena helloides* among residents and *Pieris rapae*, *Pontia beckerii*, *Colias eurytheme* and *philodice*, *Coenonympha "tullia" eryngii*, and *Plebeius acmon* among species whose ability to overwinter on Ball Mountain is strongly in doubt. A single late individual of *Papilio zelicaon* has been taken that might represent a rudimentary second brood (there is a late season flight at low elevations, and this is a hilltopping species). The single record of *Pyrgus communis* may also represent a fly-up.

Most of the summer univoltines have very long flights, those of most *Speyeria* including nearly the entire season. In *S. coronis*, males and females emerge early and mate; males then apparently die, but females disappear for several weeks in estivation then reappear; they may be common on yellow Composites in September. The hibernating Nymphalines (genera *Nymphalis*, *Polygonia*, and *Vanessa*) fly in both spring and autumn. Of them, only *V. annabella* may be partially double-brooded on the mountain. *Hesperia juba* has the same phenology as the Nymphalines and is suspected of hibernating as an adult also (Shapiro 1979). The meadow flora and fauna peak early, with many species disappearing by mid-August. On Little Shasta Meadow the only plants in flower by early September are *Polygonum douglasii* var. *austinae* Jones and a few Asters. The overall butterfly phenology is unusual, with little change in the number of species over the entire season but peaks at both ends and a trough in mid-summer. This pattern, albeit weak, is nearly the inverse of the montane pattern shown in the Sierra Nevada (cf Donner Pass, Shapiro 1975: 189).

Comments follow on the most unusual elements in the fauna. Systematic order in Table 1 and the text follows Dornfeld, 1980, the geographically closest faunistic treatment in the literature.

***Pieris napi* L.** ssp.—One fresh male collected vi.12.85 at the edge of Little Shasta Meadow. It is very heavily marked and resembles first-brood *marginalis* Scud. from the north coast. There is an endemic "*napi*" in the Warner Mountains that has a similar first brood and a lightly marked "*pallidissima*" B. & McD. second brood and occurs on boggy meadows. The affinities of this isolated *napi* population need to be clarified, because the biogeography of the complex is very difficult in northern California (Geiger and Shapiro 1986a, in press).

***Colias*.**—Agricultural, alfalfa-based populations as high as the end of York Road are hybrid swarms involving *C. eurytheme* Bdv. and *C. philodice eriphyle* Edw. Both species and hybrids are common on all the meadows and even to the summit most of the season. There is definitely breeding on *Trifolium* spp., but the phenotypes of spring animals suggest colonization from below each year, rather than overwintering in situ. By September nearly all the clover on Little Shasta Meadow is senescent.

***Anthocharis sara sara* Lucas.**—Frequent along roadsides near Little Shasta Meadow. These butterflies have pure white ground color and are indistinguishable from montane *sara* from the Trinity Alps; they are extremely distinct from both yellow Sierran *stella* Edwards and from the yellow-tinged race from the Warners, and genetically they are identical to Trinity and North Coast Range *sara* (Geiger and Shapiro 1986b, in press).

***Euchloe ausonides* Lucas.**—These dense, montane-meadow populations behave as described by Dornfeld (p. 51) for Oregon ones, flying low above sedges and forbs in the wettest parts of the meadows. This is quite unlike the usual behavior of the species in other parts of California.

***Phyciodes campestris* Behr.**—These are quite normal *campestris*, with no tendency to reduction of the pattern as in Sierran *montana* Behr. They thus resemble Trinity-Eddy specimens.

***Euphydryas*.**—Only one specimen of each species has been taken, so that subspecific assignments in both cases are very tentative and largely based on Dornfeld's application of the names. The true identity of *edithana* Strand remains uncertain. Both subspecific assignments suggest affinity with the Warners.

***Speyeri coronis* Behr.**—These are typical "blend zone" populations like those found in the Eddies, Scott Mountains, and Scott Valley as well as in much of southern Oregon.

***Speyeria callippe* Bdv.**—This is a scarce species on Ball Mountain, and the subspecific assignment is based on a short series and must be considered tentative. All our specimens are silvered, and on average they fall between *rupestris* Behr and topotypical *juba* Bdv. in facies.

***Speyeria atlantis* Edw.**—Common to abundant, flying all season. There is a remarkable, apparently endemic melanic form in both sexes—more extreme in the female—with a frequency of over 50% above the junction of roads 47N03 and 46N10, and over 70% at the summit. This form (Fig. 3a) intergrades to more or less normal *dodgei* Gunder. One specimen taken ix.5.85 has one hindwing aberrant (Fig. 3d).

***Speyeria mormonia* Bdv.** ssp.—Outside the Sierra Nevada, this species was previously known in California only from Deadfall Lakes and Mount Eddy (Shapiro, Palm, and Wcislo 1981) and from the Warners. The subspecific identities of these populations are not clear; Shapiro et al. treated the Deadfall-Eddy population as an outlier of the Oregon Cascade *erinna* Edw., but neither it nor the somewhat paler Warner phenotypes precisely matches either Cascadian or Sierran material. Three specimens were collected ix.5.85 on flowers of *Haplopappus bloomeri* about 0.8 km below Little Shasta Meadow and on the lower portion of the meadow itself. They were among

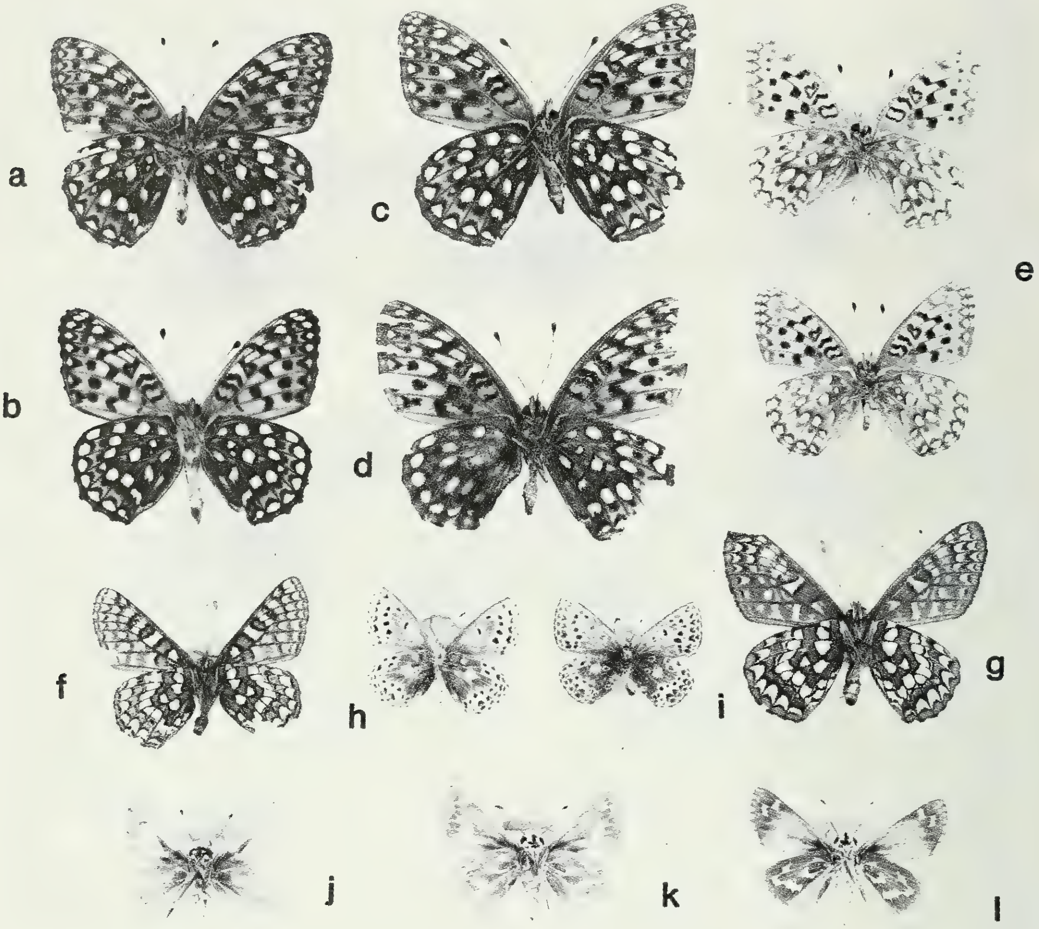

Fig. 3. Same as for Figure 2, ventral surfaces.

many other fritillaries of three species. All are very small (LFW 20-21.5 mm) and not a precise match for either Deadfall-Eddy or Warner specimens. Typical *mormonia* habitat (wet meadow) is abundant on Ball Mountain, but as in the Eddies the species appears to be rare and to emerge remarkably late in the season. The geography of *Speyeria mormonia* in far northern California promises to shed light on the history of biotic migrations in the Quaternary.

Lycaena heteronea gravenotata **Klots**.—The status of this subspecies name is controversial. Ferris and Brown (1981) gloss over any pattern of geographic distribution for spotted and unspotted hindwings in the Rocky Mountains. Dornfeld (1980) finds a definite pattern of spotted colonies within a region of generally unspotted ones. In California, the spotted morph is known *only* from Ball Mountain (Little Shasta Meadow to summit), nearby Goosenest, Warner Valley (just S. Mt. Lassen), and near Castella (J. F. Emmel, personal communication). These appear to be pure spotted populations, surrounded by pure unspotted ones. The host plant on Ball Mountain has not been determined, but a white-flowered *Eriogonum* that occurs at both Little Shasta Meadow and near the fire tower is suspected. (A member of the "*E. nudum* complex" is reportedly used at Warner Valley; J. F. Emmel, personal communication). There is no adult association with *E. umbellatum*, such as one sees consistently in the Trinities. Figures 4a, b and 5a, b show both sexes. Collectors should be aware of the possibility that further colonies exist near Mount Shasta. The possibility of sibling species cannot be discounted.

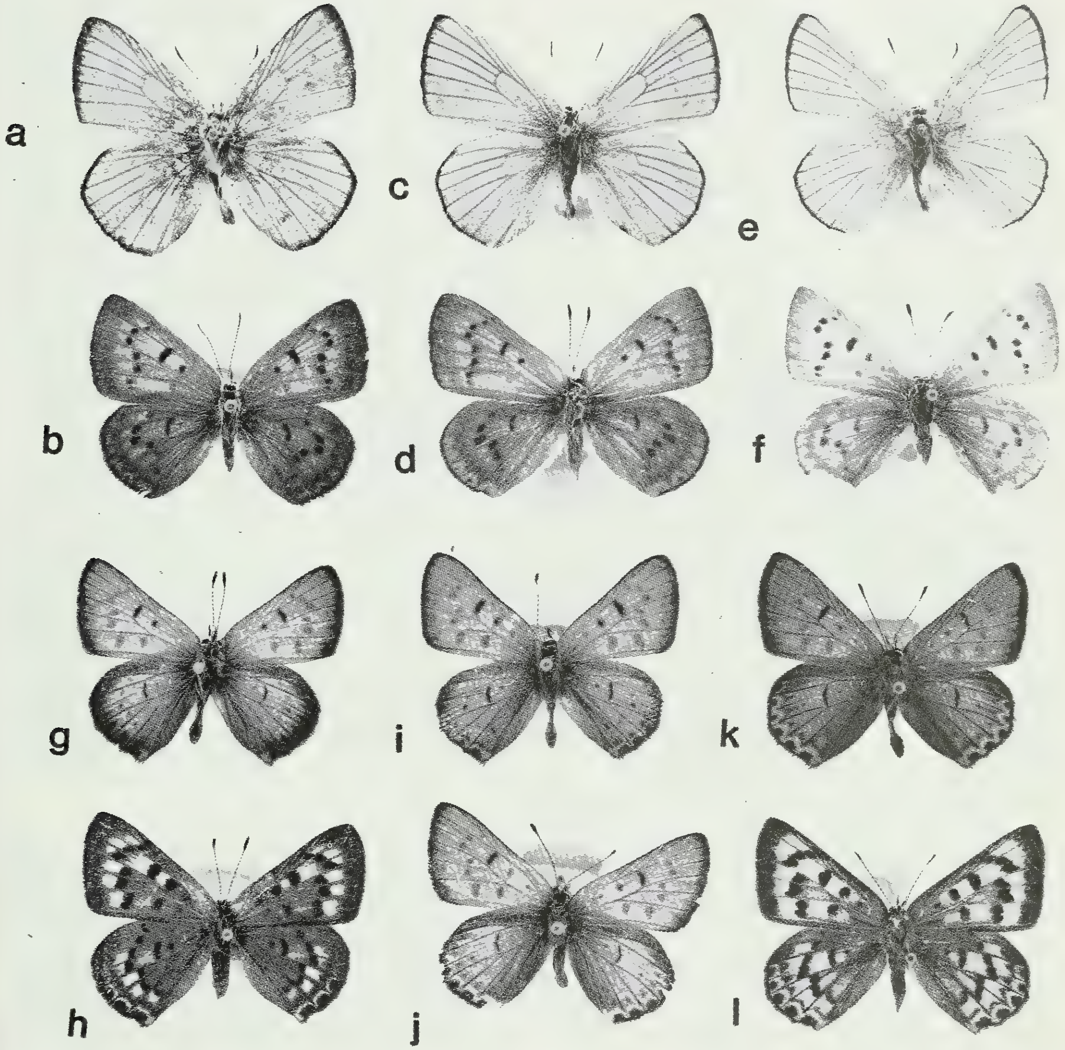

Fig. 4. Northern California *Lycaena*, dorsal surfaces: a, *L. heteronea gravenotata*, male, Ball Mountain, viii.10.83; b, same, female, Ball Mountain, viii.10.85; c, *L. h. heteronea* (?), male, Dry Lake Lookout, Siskiyou Co., viii.9.83; d, same, female, Dry Lake Lookout, viii.9.83; e, *L. h. heteronea*, male, Winnemucca Lake, Alpine Co., viii.24.83; f, same, female, Winnemucca Lake, viii.24.83; g. *Lycaena nivalis*, male, Ball Mountain, vii.15.83; h, same, female, Ball Mountain, vii.15.83; i, *L. nivalis*, Cedar Pass, Modoc Co., vi.9.85; j, *L. nivalis*, male, Winnemucca Lake, Alpine Co., viii.24.83; k, *L. nivalis* "form 1," male, Paradise Lake, Marble Mts., Siskiyou Co., vii.4.81; l, same, female, Paradise Lake, vii.4.81.

Lycaena xanthoides **Bdv.-*L. editha*** **Mead.**—*Lycaena xanthoides* is found in the Central Valley (usually near the Sacramento River), in the San Francisco Bay area, the Transverse Ranges and some areas of southern California, and apparently disjunctly as a series of montane populations from Lake County through the Mendocino Pass–Anthony Peak area, and in the Willamette Valley in Oregon. *Lycaena editha* is found in the Rockies, the Sierra Nevada, and the Cascades as a montane-to-subalpine species. From Dunsmuir to Siskiyou Summit and from Gazelle to Ball Mountain and Iron Gate Reservoir occur a series of apparently intermediate populations, generally in agriculturalized valleys. The highest elevation of these is the one on road 47N03 near Kuck's Cabin, of which strays occur as high as Little Shasta Meadow. It also seems to be the easternmost of the blend-zone populations.

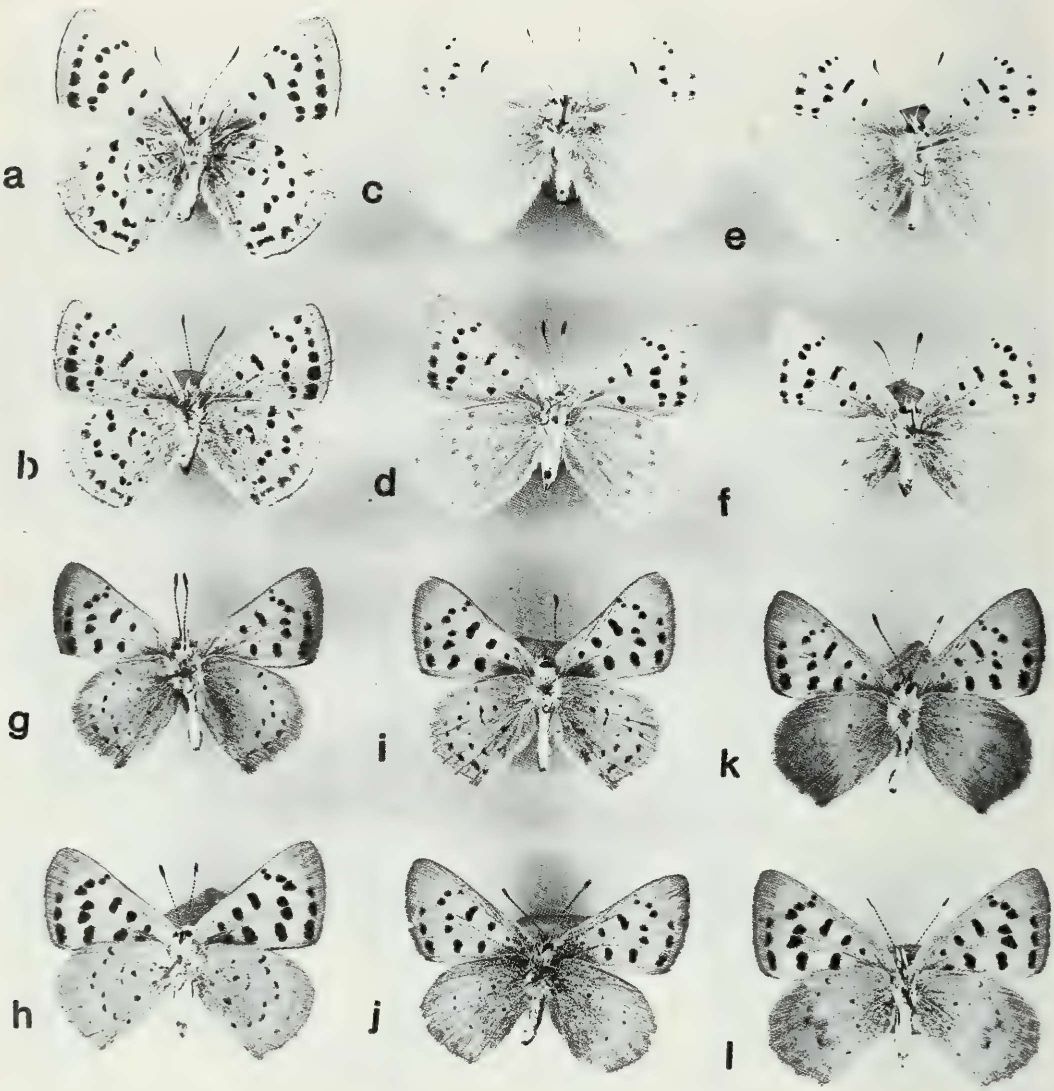

Fig. 5. Same as for Fig. 4, ventral surfaces.

Lycaena helloides Bdv.—This is usually considered a weedy lowland species, but here as elsewhere in northern California it seems to have permanent montane-meadow populations and has been seen laying on *Polygonum douglasii* var. *austinae* in September.

Lycaena nivalis Bdv.—Dornfeld (1980: 97, maps 137–138) pointed out that two "forms" of the nominal species *L. nivalis* occur in Oregon—sometimes sympatrically, sometimes not. Both also occur in northern California. Trinity-Eddy populations (Shapiro, Palm, and Wcislo 1981) are 100% "form 1" (two-toned VHW), and Ball Mountain ones are 100% "form 2" (nearly unicolorous VHW). Form 1 has not been found east of U.S. Highway 5 in California to my knowledge. Form 2 is similar, but not identical, to the form that occurs in the Sierra Nevada. Some individuals show a tendency toward the endemic, heavily spotted Warner Mountains form. All these phenotypes are shown in figures 4g-l, 5g-l. At Little Shasta Meadow eggs are laid on *Polygonum douglasii* var. *austinae*. Trinity-Eddy form 1 use *P. spergulariaforme* Meissn., a closely related species. As with *L. heteronea*, sibling species are strongly suspected.

Agriades "*glandon* Prun." ssp.—Conspecificity with the European taxa of this group is questionable. As noted by Shapiro, Palm, and Wcislo (1981), northern California populations are considerably darker and more heavily spotted beneath than Sierran *podarce* Felder (the usual usage, the type locality being simply "California"). The type of Boisduval's *nestos*, from Oregon, should be examined to determine its consubspecificity with these populations. Ball Mountain "*glandon*" average darker and more heavily spotted beneath than any other North American population known to me and seem to represent the extreme end of a cline (Figs. 2,3h,i).

***Hesperia* "*comma* complex."**—Again, the use of the name *comma* L. seems questionable. On the other hand, it is unclear what strictly Nearctic names apply to our handful of Ball Mountain specimens, which vary in complex ways between the taxa *oregonia* Edwards and *harpalus* Edwards; there is too little material (mostly from thistles along the roads, where *Hesperia* is enormously outnumbered by *Ochlodes sylvanoides* Bdv.) to say whether the phenotypes are altitudinally stratified as in the Trinities, or scrambled as on Mount Eddy. The range of variation is shown in figures 2, 3j-l.

DISCUSSION

This fauna of 68 species is remarkably rich for a forested, isolated mountain area that is surrounded by unforested lowlands. The major elements of biogeographic interest are enumerated below.

1. *Endemics*.—These include the melanic forms of *Agriades* "*glandon*" and *Speyeria atlantis*, and probably *Speyeria mormonia; Lycaena heteronea gravenotata* is a near-endemic (actually, most of the *Speyeria* species on Ball Mountain show local peculiarities, which, however, are less conspicuous than the melanism of *S. atlantis*).

2. *Regional Rarities*.—Species rare and local in northern California that occur in the study area include *Incisalia fotis, Mitoura spinetorum, Lycaena arota,* and *Erynnis icelus* (*L. arota* is relatively common in the Trinities but flies quite late, as here; it seems rare elsewhere in the region). *Polygonia faunus rusticus* is rare throughout its range; *Glaucopsyche piasus* nearly so.

3. *Intermediate or Transitional Populations*.—*Lycaena xanthoides–editha; Hesperia* "*comma* complex"; *Colias* hybrid swarms (common in agricultural alfalfa but not otherwise recorded in montane meadows regionally).

4. *Regionally Common Species, Rare on Ball Mountain*.—These include *Neophasia menapia, Phyciodes campestris, Chlosyne hoffmanni, Satyrium saepium, Plebeius "idas," Everes amyntula, Glaucopsyche lygdamus*, the *Hesperia* "*comma* complex," and *Pyrgus communis*.

5. *Range Extensions with Westward Affinities*.—*Anthocharis sara.*

6. *Range Extensions with Eastward (Warner Mountains) Affinities*.—Possibly both *Euphydryas*; possibly *Lycaena nivalis*.

7. *Absences.* These deserve special enumeration; they are species that, on a regional basis, would be considered likely on Ball Mountain but have not been found.

7a. *Alpine and Barren-Ground Species*.—Suitable habitats are clearly not present for *Papilio indra* Reak., *Parnassius phoebus sternitzkyi* McD., *Pontia sisymbrii* Bdv., and *Euchloe hyantis* Edw. *Callophrys lemberti* Tilden and *Philotes battoides* Behr may also fit in this category, though potential host plants are present.

7b. *Species of Special Habitats Apparently Absent or Too Isolated*.—*Lycaena mariposa* Reak. is common at the edges of boggy meadows in the Lodgepole Pine zone farther west (Trinities and Eddies, Scott Mountains). Perhaps the meadows on Ball Mountain are insufficiently boggy. The host plant remains unpublished but is reported to be *Vaccinium* spp. (G. Pratt, in litt.) This plant is not recorded on Ball Mountain. *Euphyes vestris* Bdv. has been found in several isolated boggy meadows (e.g., Scott Mountain Summit Bog). Its host plant, *Cyperus*, occurs near Little Shasta Meadow, but the colony is perhaps too small and isolated to support the skipper.

7c. *No Apparent Explanation*.—These include *Chlosyne palla* Bdv., *Satyrium fuliginosum* Edw., *S. sylvinus* Bdv., *S. californica* Edw., *Incisalia iroides* Bdv., *Philotes enoptes* Bdv., *Thorybes mexicana nevada* Scud./*aemilia* Skin., and *Polites sabuleti* Bdv. Several of these are regionally rare or local (*fuliginosum, sylvinus, californica, iroides*). But *Polites sabuleti* is the single most common butterfly in the Trinities and Eddies (Shapiro,

TABLE 2. Composition by family of some regional butterfly faunas.

Family	Trinity Alps[a]	Mt. Eddy[a]	Crater Lake[b]	Ball Mountain
Papilionidae	7	5	4	4
Pieridae	14	7	9	9
Satyridae	4	3	4	1[c]
Danaidae	1	1	1	1
Nymphalidae	31	25	25	24
Riodinidae	1	1	0	0
Lycaenidae	32	27	26	21
Hesperiidae	25	11	11	8
Totals	115	80	80	68

[a] Shapiro, Palm & Wcislo 1981.
[b] Tilden & Huntzinger 1978.
[c] *Oeneis nevadensis* may also occur.

Palm, and Wcislo 1981). It occurs on the N slope of Mt. Shasta and, at low density, in the agricultural lands both east and west of Ball Mountian; there appears to be no population adapted to montane meadows in the Little Shasta Country. This is not surprising in one sense: there is no place known where both *Ochlodes sylvanoides* and *Polites sabuleti* are common in northern California; their abundances tend to be inversely correlated, and *sylvanoides* is the commonest skipper on Ball Mountain.

7d. *Biennials.—Oeneis nevadensis* Feld. & Feld. has a two-year life cycle in much of its range, flying only in even-numbered years. Thus, if it occurs (in the lower montane coniferous forest) on Ball Mountain it would have been missed by sampling in 1983 and 1985. It is the only known biennial butterfly in the region.

A final question is that of the faunal balance. As revealed in Table 2, the family breakdown of the Ball Mountain fauna is basically consistent with other regional faunas, though slightly impoverished in Hesperiidae. What does not emerge from these data is the enormous biomass of the genus *Speyeria*, whose members are overwhelmingly dominant over virtually all habitats on Ball Mountain. This is not the only such place in northern California: Anthony Peak (Mendocino County), for example, is another. But even the casual visitor cannot help but notice how all other butterflies appear rare in comparison to the large fritillaries. Since all of them presumably feed on the genus *Viola*, which is neither unusually conspicuous nor unusually diverse on Ball Mountain, their abundance poses an ongoing ecological problem.

ACKNOWLEDGMENTS

Some studies on Ball Mountain have been carried out under California Agricultural Experiment Station project CA-D*-AZO-3994-H, "Climatic Range Limitation of Phytophagous Lepidopterans." I cordially thank my fellow collectors on the mountain: Bill Overton, Adam Porter, Virginia Pickles, Cecile La Forge, Hansjurg Geiger, and Iris Bugmann, as well as Dr. John Emmel for information on *Lycaena heteronea gravenotata* and G. Pratt for information on *L. mariposa*. Mr. More, occupant of the last house on York Road, was kind enough to pull a University of California pickup truck out of a sand pit in 1985. Had he not done so, there would have been no 1985 data.

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COMPARATIVE HABITAT AND COMMUNITY RELATIONSHIPS OF *ATRIPLEX CONFERTIFOLIA* AND *SARCOBATUS VERMICULATUS* IN CENTRAL UTAH

Jack D. Brotherson[1], Lars L. Rasmussen[2], and Richard D. Black[1]

ABSTRACT.—Thirty-four study sites were established in shadscale (*Atriplex confertifolia* [Torr. & Frem.] Wats.) and greasewood (*Sarcobatus vermiculatus* [Hoov. Torr. in Emory) communities bordering Utah Lake in central Utah. Differences in species composition, vegetation, and soil characteristics were assessed. Significant differences in soil factors between the two communities were found for sand, calcium, manganese, zinc, and copper. Soluble salts and sodium concentrations were generally higher in the greasewood type, but differences were not significant. Major differences were found in understory species, with burr buttercup (*Ranunculus testiculatus* Grantz) showing significantly greater cover in the shadscale community and cheatgrass (*Bromus tectorum* L.) showing significantly greater cover in the greasewood community.

Shadscale (*Atriplex confertifolia* [Torr. & Frem.] Wats.) and Greasewood (*Sarcobatus vermiculatus* [Hook.] Torr. in Emory) are dominants of plant communities that cover vast areas of the Great Basin and are thus important components of our western rangelands. Recent research on these species has considered soil moisture relationships (Branson et al. 1976), evolution (Stutz 1978), phenology (roundy et al. 1981, Everett et al. 1980), faunal associates (Csuti 1979, Feldhamer 1980), grazing effects (Fetcher 1981), physiology (Caldwell et al. 1977), production (Van Epps et al. 1982), and successional relationships (Vasek and Lund 1980, Wallace and Romney 1980). However, there is a lack of information from central Utah concerning differences in community and habitat requirements of shadscale and greasewood. The purpose of this study was to compare habitats of shadscale and greasewood dominated sites in central Utah. Such information is valuable when attempting to manage those species in relationship to their use as forage for sheep on our winter ranges.

STUDY AREA

Thirty-four study sites were sampled in shadscale and greasewood communities bordering Utah Lake, Utah (Fig. 1). Fifteen sites were studied in shadscale communities and nineteen in greasewood communities.

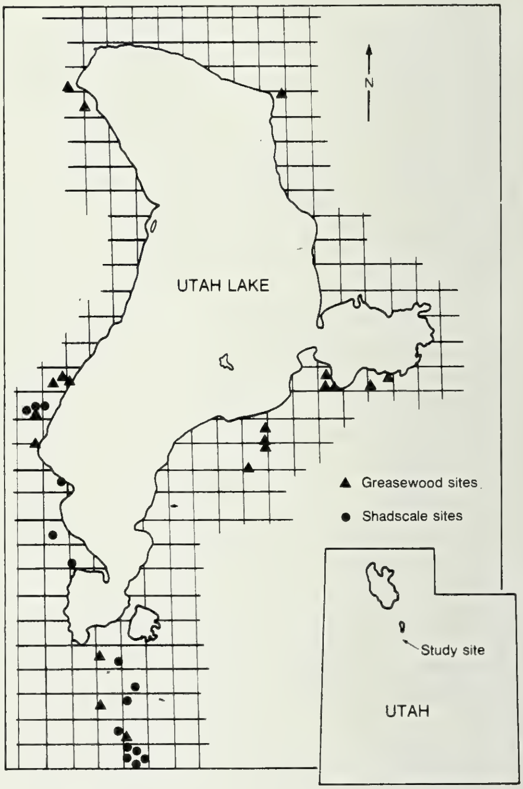

Fig. 1. Map showing the location of the 34 study sites near Utah Lake in central Utah.

Shadscale communities are generally located on the west side of Utah Lake below the sagebrush zone and above or parallel to the greasewood zone. The overstory component of this community is dominated by shadscale. The understory is composed primarily of two introduced species, burr buttercup (*Ranunculus testiculatus*) and cheatgrass (*Bromus tectorum*).

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Greasewood communities are found around the entire perimeter of Utah Lake but are best developed along the western shore. Overstory in this community is dominated by greasewood, and the understory is dominated by burr buttercup and cheatgrass. Both community types serve as winter range and spring lambing areas for several thousand head of sheep each year.

Climatic conditions at the study sites are characterized by hot dry summers and cold winters. Average annual precipitation varies from 190 to 290 mm, with 60% falling in the winter and early spring months. The hottest month of the year is July, with an average of 33 C; the coldest month is January, with an average of 3 C. The frost-free period for the area ranges from 132 to 170 days (Swenson et al. 1972).

Methods

Study areas were selected to represent a range of environmental conditions in shadscale and greasewood communities of central Utah. Once a site was located, a 10 x 10 m macroplot (0.04 ha) was randomly located within each area. Elevation, percent slope, slope position, and soil erosion were noted for each site. Each plot was subsampled with 20 0.25m^2 quadrats (microplots) stratified across the macroplot in five rows of four quadrats each. Data were taken during May and June 1980.

Total living cover, plant cover by life form, litter, exposed rock, and bare ground were estimated at each microplot following ocular procedures suggested by Ostler (1980). Cover of individual plant species encountered was also estimated using cover class categories suggested by Daubenmire (1959). All species occurring within a macroplot but not in any microplots were listed and given a percentage cover value of 0.01. All species encountered were classified as to life form, longevity, and whether native or introduced in the Utah flora.

Three soil samples were taken in each macroplot (from opposite corners and the center) from the top 20 cm of soil and later combined for laboratory analysis. This depth was considered adequate based on Ludwig's results (1969), which showed that the surface decimeter of soil yields 80% of the information useful in correlating plant response with concentrations of essential mineral nutrients in the soil. Studies by Holmgren and Brewster (1972) also showed that greater than 50% of the fine roots are found in the top 15 cm of soil profiles in desert shrub communities in western Utah.

Soil samples were analyzed for texture (Bouyoucos 1951), pH, soluble salts, mineral composition, and organic matter. Soil pH was determined with a glass electrode pH meter. Soluble salts were determined with a Beckman electrical conductivity bridge. Exchangeable calcium, magnesium, potassium, and sodium were extracted from soils with DTPA (diethylene triamine-penta-acetic acid) (Lindsay and Norvell 1969). A Perkin Elmer Model 403 atomic absorption spectrophotometer was used to determine individual ion concentrations (Isaac and Kerber 1971). Phosphorus was extracted with sodium bicarbonate (Olsen et al. 1954). Nitrogen analysis was made using macro-Kjeldahl procedures (Jackson 1958). Organic matter was estimated from total carbon using methods described by Allison et al. (1965).

Means, standard deviations, and coefficients of variation were determined for each biotic or abiotic variable across the 34 sampling plots. Prevalent species were determined following Warner and Harper (1972) on the basis of cover values. One-way analysis of variance was used to detect significant differences between the two communities with reference to 18 different soil variables. Student's t-test was used to detect significant differences in site characteristics and biotic factors between the two communities. Taxonomic determinations for all plant species included in our study follow Arnow et al. (1980).

Results and Discussion

Significant differences between factors of the shadscale and greasewood communities near Utah Lake existed for only two of the

TABLE 1. Means, standard deviations, and coefficients of variation of general site characteristics for shadscale and greasewood communities around Utah Lake (N = 34).

	Shadscale			Greasewood		
Site characteristics	Mean	S.D.	C.V.	Mean	S.D.	C.V.
Elevation	4524.53	17.94	0.003	4530.75	45.75	0.01
Percent slope	.73	1.44	1.97	0.95	1.76	1.28
[a]Slope position*	1.47	0.83	0.57	2.15	0.93	0.43
[b]Erosion	0.00	0.00	0.00	0.05	0.22	4.40
Percent litter cover**	5.20	3.90	0.75	2.95	4.33	1.47
Percent exposed rock	0.00	0.00	0.00	0.02	0.07	3.39
Percent exposed soil	16.07	14.65	0.91	12.56	11.33	0.90

[a]Slope position is defined as 1 = top of slope, 2 = midslope, 3 = bottom of slope.
[b]The erosion index runs from 0 to 3, with 0 indicating no erosion and 3 heavy.
*Significant differences between means at 0.10 level.
**Significant difference between means at 0.05 level.

TABLE 2. Means, standard deviations, and coefficients of variation of cover of prevalent species in shadscale and greasewood communities around Utah Lake (N = 34).

	Shadscale			Greasewood		
Species	Mean	S.D.	C.V.	Mean	S.D.	C.V.
Atriplex confertifolia	16.80*	8.71	0.52	0.24*	0.89	3.70
Bromus tectorum	10.77*	9.25	0.86	35.38*	27.69	0.78
Cardaria draba	0.00	0.00	0.00	5.68*	14.74	2.60
Ephedra viridis	2.01*	6.83	3.40	0.00	0.00	0.00
Halogeton glomeratus	1.89*	4.23	2.24	1.24	5.48	4.42
Hordeum leporinum	0.00	0.00	0.00	5.62*	14.74	2.62
Kochia americana	5.67*	8.05	1.43	0.00	0.00	0.00
Kochia scoparia	1.75*	6.27	3.58	7.47*	13.13	1.76
Lepidium perfoliatum	8.71*	6.86	0.79	7.82*	8.45	1.08
Ranunculus testiculatus	60.77*	25.78	0.42	23.25*	25.99	1.11
Salsola iberica	0.01	0.04	4.00	3.26*	6.55	2.00
Sarcobatus vermiculatus	2.22*	3.11	1.40	28.88*	14.62	0.51
Sitanion hystrix	0.99	1.56	1.58	2.39*	5.07	2.12
Suaeda calceoliformis	0.01	0.03	3.00	3.75*	13.11	3.50
Suaeda torreyana	1.35*	2.40	1.77	2.69*	6.10	2.27

*Prevalent species

eight general site variables considered (i.e., slope position and percent cover, Table 1). Shadscale had greater litter cover and tended to occupy upper slope positions, whereas greasewood was found at midslope positions.

Shadscale and greasewood communities had six prevalent species in common (Table 2). Cover of annual plants was 66% and 52% in the shadscale and greasewood communities, respectively (Table 3). These cover values represented 72% and 65%, respectively, of the total living cover of those two communities. The cover values for burr buttercup and cheatgrass were of particular interest. The greasewood and shadscale communities considered herein had been heavily impacted for many years by domestic grazing animals (Table 3). Such sustained overuse would open up areas within the community and allow these introduced species to invade and develop high cover values. The area is used as late winter and early spring sheep range, and sustained overuse is the suggested cause for deteriorated range condition at most of the sites (Brotherson and Evenson 1982). Grazing estimates were based on the condition of plants and soils and their relative responses to grazing (Stoddart et al. 1975).

The shadscale community had significantly greater burr buttercup cover and significantly less cheatgrass cover than the greasewood community. Burr buttercup (Table 2) contributed 60% cover, whereas cheatgrass contributed only 10% in shadscale plots. Conversely, the greasewood community contained significantly greater amounts of cheatgrass. Other annual forbs, (Belvedere summer cypress, *Kochia scoparia*, Haloge-

TABLE 3. Means, standard deviations, and coefficients of variation for biotic factors in shadscale and greasewood communities (N = 34).

	Shadscale			Greasewood		
	Mean	S.D.	C.V.	Mean	S.D.	C.V.
Total living cover	79.4	14.50	0.18	80.7	16.12	0.20
% Shrub cover	14.1	6.00	0.43	20.3	10.13	0.50
% Subshrub cover**	8.4	12.87	1.54	2.9	8.71	2.93
% Perennial forb cover**	0.0	0.00	0.00	3.3	7.27	2.23
% Perennial grass cover**	2.2	2.15	4.91	5.3	8.05	1.53
% Annual grass cover***	8.4	5.90	0.71	26.2	21.15	0.81
% Annual forb cover***	57.7	21.06	0.37	29.3	22.67	0.77
% Total annual cover***	66.1	19.50	0.30	52.2	21.53	0.41
% Cryptogam cover*	9.4	6.61	0.71	6.8	6.85	1.01
Diversity	1.9	0.42	0.22	2.2	0.48	0.22
Number of species/quadrat	0.5	0.12	0.28	0.5	0.16	0.31
Number of species/stand	9.1	2.71	0.30	10.3	3.21	0.31
Number of native species/stand	4.9	1.92	0.39	5.5	2.93	0.53
Number of introduced species/stand	4.2	1.42	0.34	4.8	1.70	0.36
Percent of flora:						
Native species	52.5	12.67	0.24	51.7	16.49	0.32
Introduced species	47.5	12.67	0.27	48.4	16.49	0.34
Percent of total cover:						
Native species**	27.9	19.08	0.68	34.6	17.37	0.50
Introduced species**	72.1	19.08	0.26	65.4	17.37	0.27
Grazing impact	2.5	0.74	0.29	2.5	1.00	0.40

*Significant difference between means at 0.10 level.
**Significant difference between means at 0.05 level.
***Significant difference between means at 0.01 level.

ton–*Halogeton glomeratus*, and clasping pepperweed, *Lepidium perfoliatum*) showed different patterns of distribution. Halogeton and clasping pepperweed were evenly distributed in both communities, whereas Belvedere summer cypress showed much greater cover in the greasewood type.

Other grass species—rabbit barley *(Horidum leporinum)* and bottlebrush squirreltail (*Sitanion hystrix*)—showed patterns similar to cheatgrass. Reasons for these relationships are unknown. Edaphic factors may be partially responsible for site selection of the two annuals (burr buttercup and cheatgrass). This is shown in the distribution patterns of the two species when their cover values are plotted against the different soil factors (Fig. 2). As shown, the two species exhibit different patterns with respect to percent sand, percent silt, percent fines, pH, nitrogen, calcium, iron, zinc, and copper. The species patterns with respect to the textural classes appear as mirror images of each other; therefore, the relationship is probably due to species interactions rather than cause and effect with respect to the soil factor itself. The species distribution patterns with respect to pH, nitrogen, calcium, iron, zinc, and copper are more disjunct and, therefore, may suggest cause and effect relationships. When we examine these factors with respect to their distribution between the two community types, the differences in calcium, zinc, and copper are shown to be significantly different. However, the lack of significant differences between the majority of the soil factors measured and the rather large coefficients of variation attached to these same variables suggest that the exhibited differences in distribution may be a function of which species first invaded and became established. Once established, species such as burr buttercup and cheatgrass may be highly competitive to other species. Competitive relationships between these two annuals would certainly follow invasion and may, therefore, be responsible for the observed distributions. Burr buttercup has been suspected to be allelopathic (an inhibitor of seed germination of other species through release of harmful chemicals into the soil) (Buchanan et al. 1978). Further evidence of the competitive nature of burr buttercup can be seen by examining the prevalent species lists for the two community types (Table 2). The greasewood type contained six prevalents that exhibited much greater cover values

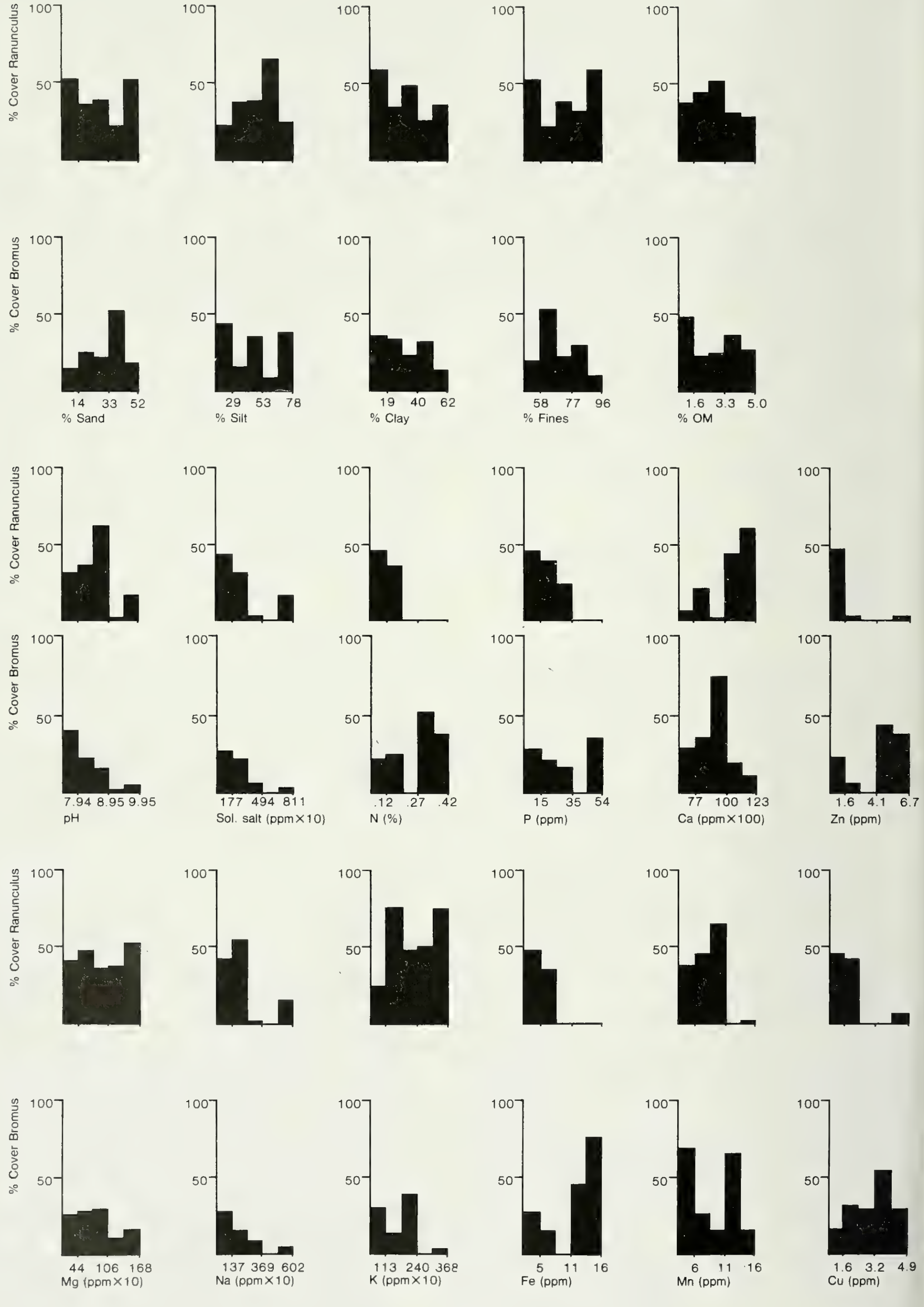

Fig. 2. Cover of *Ranunculus testiculatus* and *Bromus tectorum* plotted against major soil gradients of study sites.

TABLE 4. Means, standard deviations, and coefficients of variation of observed soil characteristics in shadscale and greasewood communities.

	Shadscale			Greasewood		
Soil characteristics	Mean	S.D.	C.V.	Mean	S.D.	C.V.
Percent sand*	16.53	8.43	0.51	27.33	16.15	0.59
Percent silt	43.20	8.58	0.20	39.90	15.48	0.39
Percent clay	40.27	10.50	0.26	32.78	12.38	0.33
Percent fines*	83.47	8.43	0.10	72.68	16.15	0.22
Percent organic matter	2.57	0.86	0.33	2.66	1.00	0.38
pH	8.06	0.90	0.11	8.21	0.60	0.07
Soluble salts (ppm)	614.20	259.03	0.42	1502.35	2156.21	1.44

*Significant difference at .05 in the means.

TABLE 5. Means, standard deviations, and coefficients of variation of soil nutrient in shadscale and greasewood communities.

	Shadscale			Greasewood		
Soil nutrient	Mean	S.D.	C.V.	Mean	S.D.	C.V.
Percent nitrogen	0.11	0.04	0.37	0.13	0.09	0.72
Phosphorus (ppm)	13.70	5.62	0.41	18.60	11.31	0.61
Calcium (ppm)***	11146.70	518.23	0.05	9062.30	1675.29	0.18
Magnesium (ppm)	786.90	355.39	0.45	607.80	409.31	0.67
Sodium (ppm)	613.10	331.78	0.54	1031.20	1566.45	1.52
Percent Na saturation	4.34	2.20	0.51	8.64	12.14	1.40
Potassium (ppm)	1364.30	772.01	0.57	921.00	598.08	0.65
Iron (ppm)	4.30	0.98	0.23	5.80	3.56	0.62
Manganese (ppm)*	6.60	1.56	0.24	8.70	3.54	0.41
Zinc (ppm)*	0.62	0.29	0.47	1.70	1.75	1.06
Copper (ppm)**	1.30	0.38	0.30	2.20	1.22	0.55

*Significant at .05 level in the means.
**Significant at .01 level in the means.
***Significant at .001 level in the means.

on the greasewood sites than on the shadscale sites. The shadscale community, on the other hand, had only two prevalents that showed greater cover on the shadscale than on the greasewood sites. Both of these species were shrubs. If burr buttercup is as allelopathic to cheatgrass as it is to other grass species, then burr buttercup should have a competitive advantage. However, further study is needed concerning the factors involved in the distribution of these two introduced annuals before the question can be fully answered.

Soils from the greasewood community had significantly more sand than soils from shadscale stands (Table 4). No significant differences were found for percent silt or percent clay in these communities, but, when combined, silt and clay (fines) were significantly greater in the shadscale community. We suspect that the sifting effects of currents at high water levels of the lake in the distant past, may have been responsible for larger percentages of sands in the greasewood type in this study.

Mineral nutrient concentrations in the shadscale stands were greater than have been previously reported (El-Ghonemy et al. 1980). Sodium, zinc, and nitrogen were approximately 1.2 times greater in our study area, manganese was 3.4 times greater, and copper was 8.1 times greater. Even larger differences were found for phosphorus and iron concentrations, which were approximately 26 times greater in our study area than in the Mojave Desert areas studied by El-Ghonemy et al. (1980). Calcium and magnesium concentrations combined were 6.8 times greater in our study area. Potassium was the only ion reported to have greater concentrations in Nevada than in our study area in Utah. Comparable soil data were not found in the literature for comparison with our results from greasewood sites.

Significant differences between shadscale and greasewood communities at the Utah Lake site were found for calcium, manganese, zinc, and copper (Table 5). Calcium was sig-

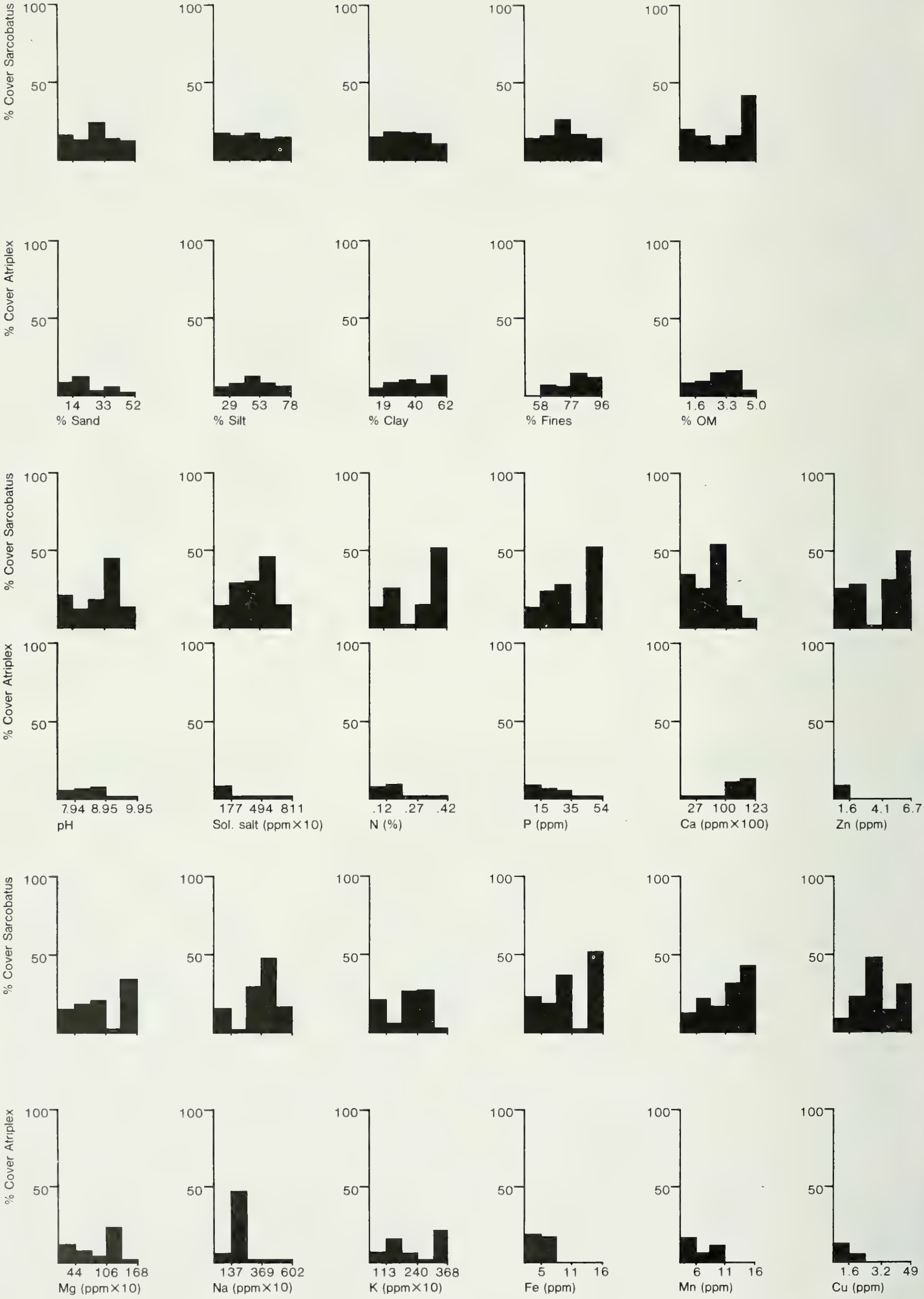

Fig. 3. Cover of *Sarcobatus vermiculatus* and *Atriplex confertifolia* plotted against major soil gradients of study sites.

Table 6. Species preferences indices with respect to measured soil factors.

	Species			
Site factor	*Sarcobatus vermiculatus*	*Atriplex confertifolia*	*Ranunculus testiculatus*	*Bromus tectorum*
Sand (%)	21.4	17.2	19.6	24.7
Silt (%)	42.5	42.7	44.4	40.2
Clay (%)	35.4	40.3	36.0	34.5
Fines (%)	78.0	83.1	80.4	74.7
Organic matter (%)	2.8	2.8	2.5	2.7
pH	8.2	8.2	8.2	8.0
Soluble salts (%)	1,526.4	720.2	718.4	665.2
Nitrogen (%)	.14	.12	.11	.13
Phosphorus (ppm)	21.5	14.2	23.4	15.9
Calcium (ppm)	9,343.9	11,116.1	10,729.6	9,498.7
Magnesium (ppm)	649.0	852.7	664.9	620.0
Sodium (ppm)	1,057.8	730.0	631.2	457.1
Potassium (ppm)	987.7	1,333.4	1,384.8	910.3
Iron (ppm)	6.4	4.4	4.0	5.6
Manganese (ppm)	9.3	6.5	6.9	7.9
Zinc (ppm)	1.9	.59	.75	1.7
Copper (ppm)	2.3	1.2	1.5	1.2

nificantly greater in the shadscale community. Since the shadscale sites occurred at the top of slopes and greasewood sites occupied midslope areas (Table 1), Romney and Wallace's (1980) contention that calcium tends to dominate the soluble cation complex at upland positions is supported. We suspected that total soluble salts and concentrations of sodium would be significantly greater in the greasewood community (Fireman and Hayward 1952). However, significant differences were not observed, although salt concentrations were higher at some greasewood sites. Percent sodium saturation was also greater in the greasewood community, but differences between communities was not statistically significant. This is best explained in terms of slope position. As indicated by Romney and Wallace (1980), sodium should dominate only at the bottom of slopes in closed drainage basins. In our study sites greasewood was not located within a closed drainage basin, but instead at midslope positions (Table 1).

Copper, zinc, and manganese concentrations were all significantly greater in soils from the greasewood community, which suggests that there may be greater availability of these nutrients to greasewood than to shadscale. However, since no data are available on the nutritional needs of greasewood and shadscale, no judgement can be made as to the role different concentrations might play in the distribution patterns of species within the two communities. In any event, these minerals accounted for detectable differences between shadscale and greasewood habitats in central Utah.

To better understand the microhabitat variation between greasewood and shadscale, their percent cover was plotted against the measured soil factors (Fig. 3). Variation in each soil factor (percent sand, organic matter, calcium, etc.) was considered as a gradient. Measured values for all sites were ranked and the corresponding species cover values were plotted against the gradient. This procedure allowed visualization of the point along the gradient where each species was most important as measured by percent cover. With this approach, one is able to visualize those factors that may be important in niche separation. In our case differences existed between greasewood and shadscale for soluble salts, nitrogen, phosphorus, calcium, zinc, sodium, iron, manganese, and copper. Where a species exhibits distinctive patterns with respect to a soil gradient, we may postulate some degree of cause and effect relationship. Conversely, if the species showed no patterns of restriction, but was randomly spread across the gradient, we postulate that the species distribution is probably not affected by that factor. It is possible that strong patterns may exist along a gradient and yet not be due to a causal relationship. Rather, the pattern could be due to some other environmental factor closely correlated to the gradient factor in question. In some cases, patterns in species distribution may also relate to patterns in a complex of habitat factors rather than to any single factor.

Shadscale showed rather narrow ranges of distribution with respect to the micronutrients (zinc, iron, manganese, and copper) but generally grew across the full extent of all the other gradients. Greasewood showed rather broad tolerance ranges across all the gradients (Fig. 3).

To further elucidate the relationships associated with the observed distribution patterns of the four species (burr buttercup, cheatgrass, shadscale, and greasewood), we computed species preferences indicies (Skougard and Brotherson 1979) for these species in conjunction with all measured soil factors (Table 6). As shown, the species show different preference indicies for soil factors, texture (sand and fines), soluble salts, phosphorus, calcium, sodium, potassium, iron, manganese, zinc, and copper. Whether these differences are of sufficient magnitude to be causal with respect to the observed differences in the distribution patterns of these species is not clear. However, the differences are detectable and in some cases are of sufficient magnitude that, when coupled with the other evidences discussed in this paper, they aid us in better understanding that differences do exist in the habitats of the two community types.

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TREES USED SIMULTANEOUSLY AND SEQUENTIALLY BY BREEDING CAVITY-NESTING BIRDS

Kevin J. Gutzwiller[1,2] and Stanley H. Anderson[1]

ABSTRACT.—We characterize 14 trees used simultaneously and sequentially by breeding cavity-nesting birds in Wyoming cottonwood communities. Our descriptions can be used as a management resource to enrich the diversity of breeding assemblages of these bird species.

During our three-season (1982–1984) study along the North Platte and Laramie rivers between Guernsey and Fort Laramie in Platte and Goshen counties, Wyoming, we observed various bird species nesting in decayed substrates (trees, limbs, or boles) that were simultaneously or previously occupied by other breeding hole nesters. These observations highlight behavioral phenomena that increase species richness and density in breeding communities of cavity-nesting birds. Habitat patches with individual trees that are used simultaneously or sequentially by several cavity-nesting species have higher species richness and density during the breeding season than patches without such substrates (Gutzwiller 1985). The cottonwood (*Populus*) communities we studied (and probably many other plant communities) would support fewer nesting individuals and species in the absence of repeated tree use. In this note, we characterize nesting substrates associated with the phenomena of simultaneous and sequential nesting. Our purpose is to provide habitat information useful to those who wish to improve species richness and density of cavity-nesting birds in western riparian cottonwood communities.

Only 14 of 173 (8%) active nest trees received repeated use during the three breeding seasons; 7 trees were used simultaneously, 4 were used sequentially from year to year, and 3 were used sequentially within a single breeding season (Table 1). We searched for nests and observed behavior around nests for a total of approximately 720 h; yet we detected little intraspecific and interspecific aggression near nest cavities, despite considerable overlap in habitat use (Gutzwiller 1985) and the close proximity of many nests. Once we saw a pair of American Kestrels chase an adult male American Kestrel away from their cavity. Twice we observed individual Red-headed Woodpeckers enlarging the entrances of active Downy Woodpecker nests; the latter species (a pair in each case) attacked the former continuously, and neither species nested in the cavities afterward. One other time we saw a pair of Red-headed Woodpeckers defending their nest hole by chasing several European Starlings that approached the nest entrance or the branches of the nest tree.

We attribute this general lack of aggression, in part, to an abundance of suitable cavities, not all of which were occupied each year. Most (159 of 173) (92%) of the nest substrates we examined were not used more than once or occupied by more than one species during our three-season study; those that were used more frequently (Table 1) were, presumably, more attractive to various species than other available substrates. This lack of aggression among individuals nesting in close proximity supports other reports of cavity nesters breeding harmoniously in similar circumstances (Hoyt 1957, Reller 1972, Jackson 1978). Short (1979: 25) explained that "Despite intense aggression between competitors for nesting sites, such competitors at least occasionally appear 'satisfied' once they have secured a nesting site [cavity], and there are many reports of nesting in proximity of usually aggressive nest-hole competitors. . . ." Another reason we detected little territorial aggression

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TABLE 1. Structural and floristic attributes of 14 nest trees used simultaneously and sequentially by cavity-nesting birds in southeastern Wyoming, 1982–1984.

Bird species[a]	Substrate use[b]	Tree species[c]	Nest height (m)	Diameter at breast height (cm)	Diameter at nest height (cm)	Nest locations	Nest entrance diameter (cm)	Nest entrance orientation[d]	Nest entrance bearing[e] (°)
AMKE, EUST	SIM	PLCO	9.0, 11.9	133.6	—, —[f]	limb[g]	—, —	A,A	243, 295
AMKE, EUST, REWO	SIM	PLCO	16.0, 17.8, 15.0	93.7	—, —, —	limb	—, 5.6, 7.0	A,B,B	2, 16, 49
AMKE, REWO	SIM	UNKN	7.4, 8.2	49.6	38.1, 25.4	bole	5.0, 6.0	B,A	238, 72
NOFL, EUST	SIM	PLCO	10.7, 9.7	37.3	25.4, 40.6	bole	5.8, 6.1	B,H	214, 168
REWO, EUST	SIM	UNKN	15.4, 11.0	71.2	—, —	limb	4.8, —	H,A	18, 329
HAWO, HOWR	SIM	PEWI	4.5, 5.1	22.5	17.8, 15.2	bole	5.0, 6.1	B,B	159, 159
DOWO, NOFL	SIM	PLCO	16.4, 11.4	66.2	12.7, 25.4	limb[g]	3.2, 4.7	B,B	114, 2
COGR, EUST	SEQ(C)	PLCO	18.3, 20.3	94.8	30.5, 30.5	limb	10.2, 5.6	A,B	355, 12
DOWO, DOWO	SEQ(C)	UNKN	5.0, 4.4	18.5	—, 15.2	bole	3.8, 3.6	B,B	147, 148
DOWO, DOWO	SEQ(C)	UNKN	3.7, 3.1	17.5	12.7, 12.7	bole	4.0, 3.3	B,B	283, 285
REWO, REWO	SEQ(C)	UNKN	6.7, 6.1	43.6	25.4, 33.0	limb[g]	—, —	A,A	—, —
EUST, NOFL	SEQ(S,H)	PLCO	11.5	62.2	20.3	limb	8.3	B	200
DOWO, HOWR	SEQ(S,H)	PLCO	8.3	110.0	7.6	limb	2.0	B	339
DOWO, HOWR	SEQ(S,H)	NACO	7.1	43.8	15.2	limb	3.0	B	269

[a] COGR = Common Grackle (*Quiscalus quiscula*), EUST = European Starling (*Sturnus vulgaris*), AMKE = American Kestrel (*Falco sparverius*), REWO = Red-headed Woodpecker (*Melanerpes erythrocephalus*), NOFL = Northern Flicker (*Colaptes auratus cafer*), DOWO = Downy Woodpecker (*Picoides pubescens*), HOWR = House Wren (*Troglodytes aedon*), HAWO = Hairy Woodpecker (*P. villosus*). Bird names are from American Ornithologists' Union (1983). For sequential nesting, order of mnemonics reflects nesting sequence.

[b] SIM = simultaneous, SEQ(C) = sequential use during consecutive breeding seasons, SEQ(S,H) = sequential use of the same nest hole within a single breeding season.

[c] PLCO = plains cottonwood (*Populus sargentii* Dode); UNKN = dead tree, species unknown; PEWI = peachleaf willow (*Salix amygdaloides* Anderss.), NACO = narrowleaf cottonwood (*P. angustifolia* James). Plant names are from Dorn (1977).

[d] A = entrance pointed above horizontal, H = entrance pointed horizontally, B = entrance pointed below horizontal.

[e] Adjusted for 13° easterly declination.

[f] — = data not available.

[g] nests occurred in different limbs.

might be that dominance hierarchies were established through agonistic interaction before we discovered species nesting together. Nevertheless, this probably does not account for the paucity of aggression we noticed overall, unless dominance hierarchies were established quickly, and we happened to miss seeing all of them.

Sequential use of cavities and simultaneous and sequential use of nest trees are not rare events (e.g., Brewster 1893, Bent 1948, 1950, Lawrence 1967), presumably because hole nesters (particularly secondary cavity nesters) are versatile with respect to what constitutes a satisfactory nest substrate and because such substrates are typically limited. However, repeated substrate use in our study area was not common (occurred only 8% of the time), probably because of an abundance of suitable nest trees. Our note describes tree characteristics associated with simultaneous and sequential nesting, thus focusing on features found acceptable, either synchronously or repeatedly, by as many as three species. Such acceptance of these traits increases species richness and evenness (overall diversity) in breeding communities of hole-nesting birds (Gutzwiller 1985). Our nest-tree descriptions can, therefore, be used to attract and maintain greater diversity in breeding assemblages of these species.

The Rocky Mountain Forest and Range Experiment Station of the U.S. Forest Service funded our study in cooperation with the Wyoming Cooperative Fishery and Wildlife Research Unit. We thank D. M. Finch, R. L. Hutto, M. G. Raphael, and D. E. Runde for constructive criticism on an earlier version of this paper. Our note is based on data collected in partial fulfillment of the senior author's dissertation requirements at the University of Wyoming.

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NEW SPECIES OF *MENTZELIA* (LOASACEAE) FROM GRAND COUNTY, UTAH

Barry A. Prigge[1]

ABSTRACT.—A new species, *Mentzelia* (Section *Bartonia*) *shultziorum*, of the Loasaceae (Mentzelioideae) is described. A close relationship with *M. multicaulis* (Osterh.) Darl. and *M. argillosa* Darl. is suggested based on the morphology of the flowers, leaves, and seeds.

Recent field work in Grand County of southeastern Utah has turned up two populations of an undescribed species of *Mentzelia* (sect. *Bartonia*). This section of *Mentzelia* demonstrates considerable morphological diversity and adaptability and has radiated into many of the diverse and often isolated habitats resulting from the wide range of substrate, elevation, and precipitation of the Colorado Plateau Province of eastern Utah, western Colorado, northern Arizona, and western New Mexico. Many species of this section occur on unusual substrates that are commonly unsuitable for most species because of textural properties or high concentrations of evaporites or minerals. *Mentzelia* is apparently able to exploit these habitats by escaping intense competition from species that occur on more suitable substrates. Edaphic factors and isolation are very important in their speciation and probably account for the many edaphically restricted, and often locally endemic populations of *Mentzelia* in the Colorado Plateau Province. It is from such a small, isolated, unusual substrate that this new species was discovered.

Within *Mentzelia* species recognition is based on subtle and technically difficult characters, and in the section *Bartonia* speciation has created many permutations of the available character states. This has resulted in many taxonomic headaches that standard collecting and herbarium techniques have generally been ineffective in solving. Scanning electron microscopy has greatly facilitated the delimitation of taxa by revealing the microstructure of the seed coat (Hill 1976), thus providing two new characters and several character states (radial walls straight or wavy and number and shape of papillae on tangential walls) that help elucidate the taxonomic problems. It is on the basis of micromorphological characteristics of the seed and the standard macromorphological characteristics that we recognize this new species.

Mentzelia shultziorum Prigge, sp. nov.

Fig. 1

Mentzelia multicaulis (Osterh.) Darl. affine, sed ab eo alis seminum 0.20–0.35 mm latis, foliis caulinis ovatis vel obovatis, dentibus non profundis, diversum.

Rounded, much branched, herbaceous perennial 20–30 cm tall; branches generally arching upward; pubescent with glochidiate and pointed hairs. Cauline leaves obovate, ovate or elliptic in outline, 10–30 (33) mm long, 4–20 mm wide, shallowly toothed at margin with 3–4 teeth on each side, cuneate or broadly attenuate at base, rounded obtuse or acute at apex, densely pubescent on both surfaces with both glochidiate and pointed hairs, some of which have pustulate bases. Bracts linear, lanceolate or oblanceolate; 3.5–11.5 mm long; 1.2–2 mm wide; entire or with 1 or 2 short teeth along margin. Flowers with pedicels to 2.5 mm long; calyx lobes 5, 5.4–8.5 mm long, deltoid, accuminate, 2.2–3.0 mm wide at base, calyx tube 1–1.5 mm long; petals 5, yellow, 9.2–15.5 mm long, 2.7–5.2 mm wide, acute at apex, clawed, glabrous; the next whorl within the petals of 5 petaloid stamens, broadly obovate to oblanceolate, 6.5–9.0 mm long, 1.1–3.8 mm wide, with functional anthers; stamens numerous; grading from 9 mm long for the outermost

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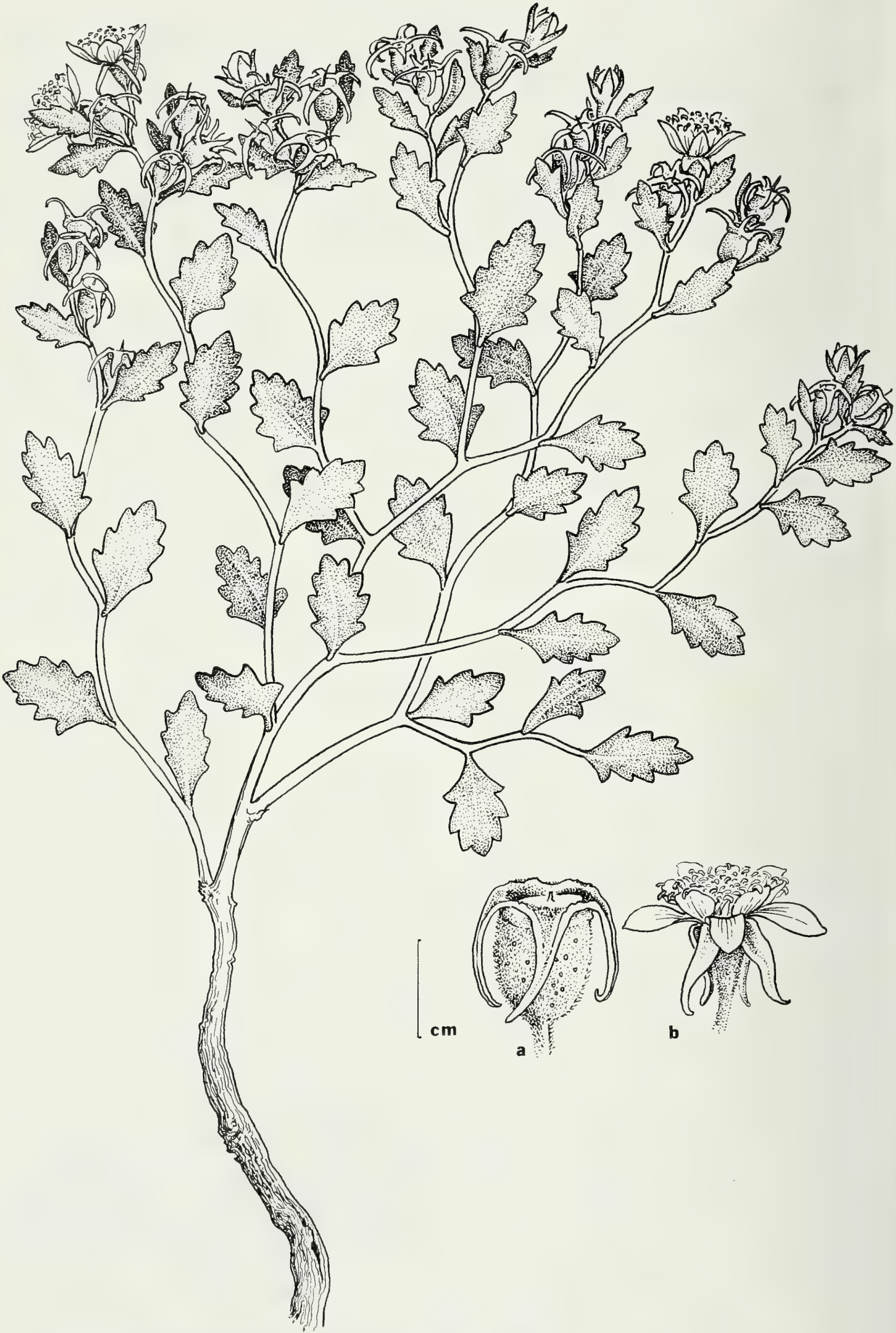

Fig. 1. *Mentzelia shultziorum* flowering branch: a, Fruit. b, Flower.

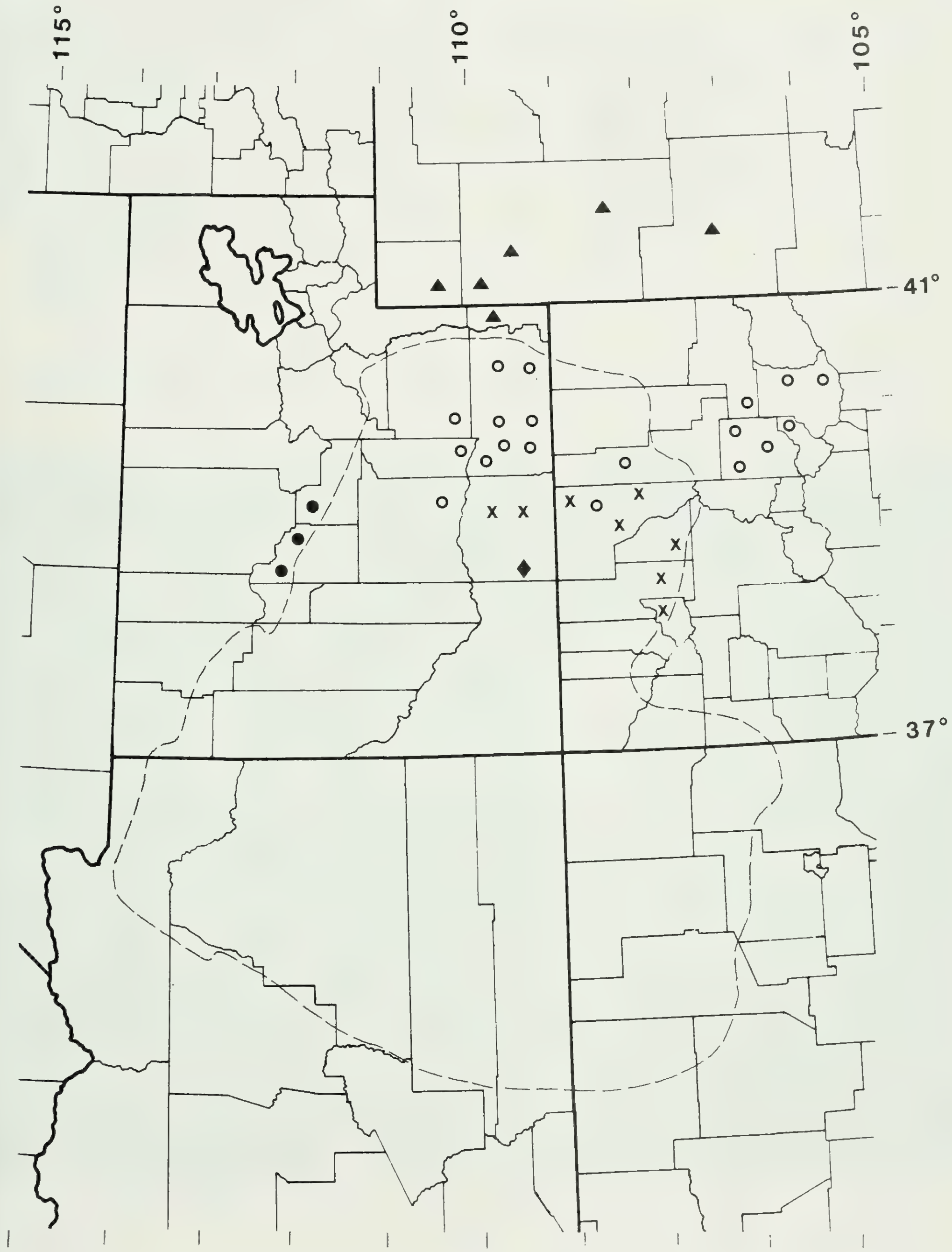

Fig. 2. Map of Utah and adjacent states showing the distribution of *Mentzelia shultziorum* (♦) and some other species that also occur on similar clay substrates: *M. multicaulis* (○), *M. argillosa* (●), *M. marginata* (X), and *M. pumila* (▲). Dashed line represents boundary of the Colorado Plateau Province.

whorl to 3.8 mm long for the innermost whorl; filaments narrow except sometimes for about 3 in the outermost whorl which are up to 1.5 mm wide; anthers 0.7–1.0 mm long; pistil 1, style 1, 7–9 mm long. Capsules broadly urceolate, 4.0–5.5 (6.0) mm long and topped by a persistent calyx, 4.2–5.0 (5.2) mm diam. Seeds lenticular, dark brown or black, 2.3–2.8

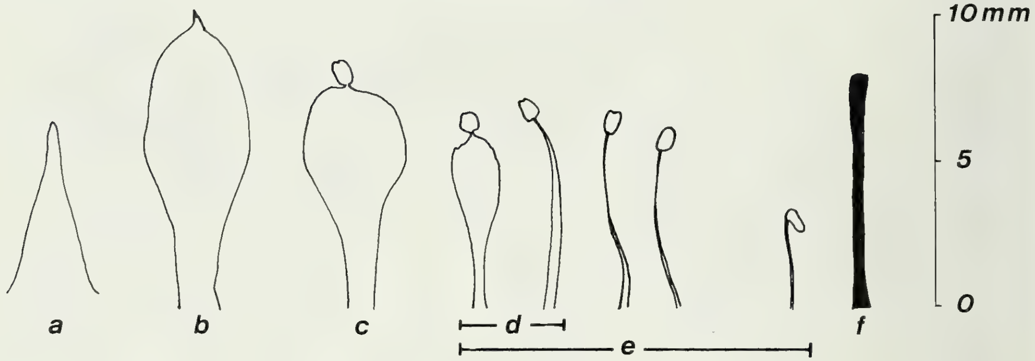

Fig. 3. Floral diagram of *Mentzelia shultziorum* representing elements of the floral whorls: a, Sepal. b, Petal. c, Petaloid stamens. d, Outermost whorl of stamens. e, Stamens from outermost to innermost whorl. f, Style.

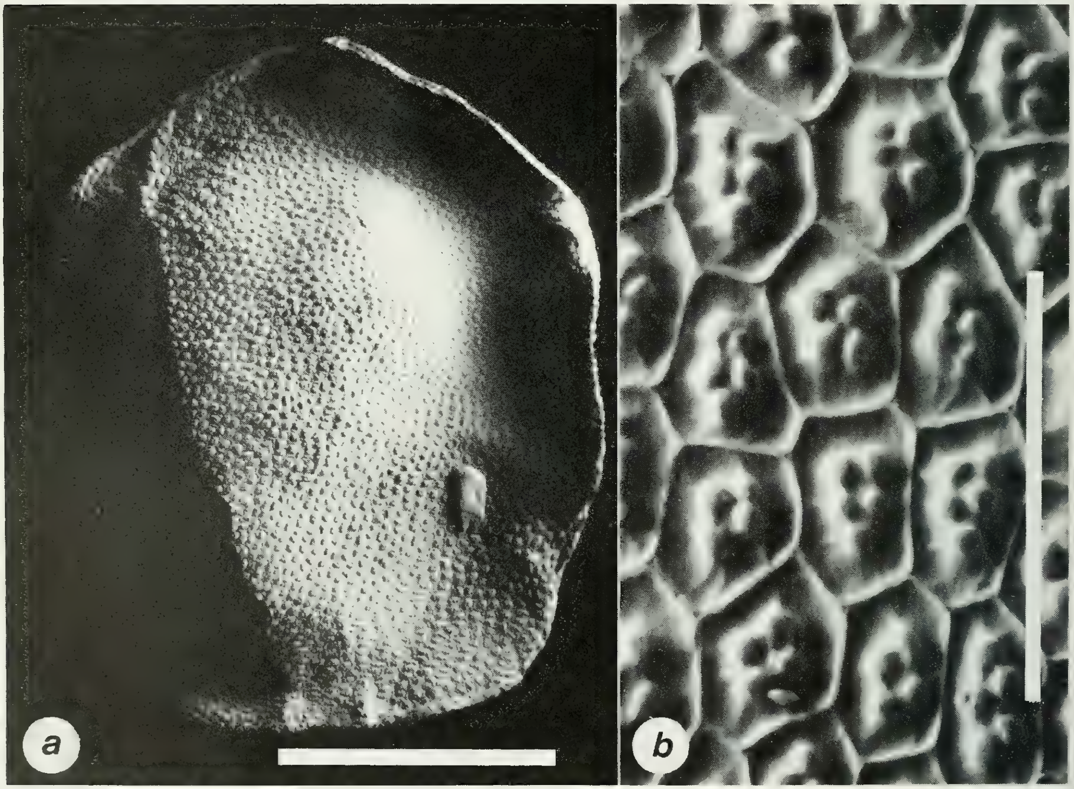

Fig. 4. Scanning electron micrograph: a, Whole seed (white bar = 1 mm). b, Seed coat cells showing straight radial walls and 2–5 papillae on tangential walls (white bar = 0.1 mm).

mm long, 1.4–3.1 mm wide, with a narrow wing 0.2–0.35 mm wide, often ridged on one or both faces, seed coat cells with straight radial walls and with 2–5 papillae on tangential walls. Flowers from July to Sept.

TYPE:—Utah. Grand Co.: 7.3 mi S of intersection of Hwy 128 and Onion Creek Rd in Fisher Valley, 11 air mi NE of Moab; Elev 5,200 ft; T24S, R24E, Sec 19., *Shultz & Shultz 2070*. Holotype: UTC. Isotypes: RSA.

SPECIMENS EXAMINED:—Utah. Grand Co.: above Onion Creek, 5,200 ft., 7.1 mi E of State Hwy 128 on Fisher Ranch Rd (38° 42′ N; 109° 15′ W), *Prigge, Shultz, & Shultz 6644*, (LA); Onion Creek drainage of Fisher Valley (11 air mi NE of Moab) 7.3 mi ESE of Hwy 128: Sec 22, T24S, R24E, 38° 42′N, 109° 15′ W, elev 5,200 ft, *Shultz, Shultz, & Prigge 9030* (UTC, LA); 9 mi NE of Moab, NW above pass between Castle Valley and Porcupine Canyon, T25S, R23E, Sec 6 NW 1/4, 4,600 ft, *Franklin 2201* (BRY).

The specific epithet is in honor of John and Leila Shultz, students of the botany of the Great Basin and Colorado Plateau, who found this new population of *Mentzelia*.

Mentzelia shultziorum is known from only two localities in Grand Co., Utah (Fig. 2). At the first locality it occurs near an old uranium and vanadium mine site on gray clay substrates of the Moss Back Member of the Chinle shale, which outcrops locally. It is restricted to steep, sparsely vegetated south-facing exposures on these substrates where alluvial and colluvial erosion rates are high. Associated species are: *Oryzopsis hymenoides, Fallugia paradoxa, Atriplex canescens*, and *Chrysothamnus nauseous*. At the second locality it is on dark red clay of the Moenkopi Formation(?) with *Atriplex, Eriogonum*, and *Ephedra*.

Mentzelia shultziorum possesses no characteristics that are not found in other species of *Mentzelia* (Sect. *Bartonia*) in Utah. However, the combination of characteristics is unique, and its relationships within the section *Bartonia* are not entirely clear. Seed shape, which is lenticular with a narrow wing 0.2–0.35 mm wide (Fig. 4), is similar to that of *M. pumila*; the seed coat cells, which have straight radial walls and 2–5 papillae on tangential walls (Fig. 4), are like those of *M. pumila* (Nutt.) T. & G. as well as *M. multicaulis* (Osterh.) Darl. and *M. argillosa* Darl.; the floral parts, which are of 5 obovate, glabrous petals and 5 obovate, petaloid stamens (Fig. 3), are like those of *M. multicaulis* and *M. argillosa* (to a lesser extent); and the leaves, which are obovate to ovate and shallowly toothed, are similar to *M. marginata* (Osterh.) Thompson & Prigge or *M. pterosperma* Eastw. Based on floral (petal shape, vestiture, and size; petaloid stamens presence/absence), seed (size, winged, seed coat cell radial walls straight or wavy and tangential wall papillae), and cauline leaf (shape and size) characteristics, *Mentzelia shultziorum* is phenetically close to *M. multicaulis* and *M. argillosa* (perhaps closer to the latter) and is probably closely related to these two species. Chromosome counts and hybridization studies will have to be done to confirm its relationship to these two species.

ACKNOWLEDGMENTS

I thank John and Leila Shultz for their help in collecting *M. shultziorum*, John Shultz for the Latin diagnosis, Henry J. Thompson for his helpful suggestions and discussions and for the use of his file of SEM micrographs of *Mentzelia* seeds, and Kaye Thorne for the illustration of *M. shultziorum*.

LITERATURE CITED

HILL, R. J. 1976. Taxonomic and phylogenetic significance of seed coat microsculpturing in *Mentzelia* (Loasaceae) in Wyoming and adjacent western states. Brittonia 28: 86–112.

UTAH FLORA: JUNCACEAE

Sherel Goodrich[1]

ABSTRACT.— A revision of the rush family, Juncaceae is presented for the state of Utah. Included are 28 taxa in two genera. Keys to genera and species are provided, along with detailed descriptions, distributional data, and other comments. No new taxa or combinations are proposed.

This paper is another in a series of works leading to a definitive treatment of the flora of Utah. The rush family as represented in Utah is rather small in comparison to some other families, but plants of the family are abundant throughout mesic and wet places of the state. Floral structures are reduced and uniform, and identification often entails observation of such minute features as tailed appendages on seeds. However, the taxa seem quite well marked and mistakes in identification do not seem so common as in some other families with reduced and uniform floral features, such as Salicaceae, Apiaceae, or Chenopodiaceae.

Members of the family are more or less comparable in palatibility to grasses and sedges, and they are abundant enough to be of importance to the grazing of domestic livestock and to big game animals.

As in preceding parts of this series, there are two numbers at or near the end of the discussion of each taxon. The first number, in Arabic numerals, indicates the number of specimens from Utah seen in the preparation of this work. The second number, in Roman numerals, indicates the number of specimens collected by the author from the state.

ACKNOWLEDGMENTS

Appreciation is expressed to the curators of the following herbaria of Utah: Brigham Young University, Provo; Forest Service Herbarium, Ogden; Garrett Herbarium, University of Utah, Salt Lake City; Intermountain Herbarium, Utah State University, Logan. I appreciate the loan of specimens from each of these herbaria. These specimens are the basis of this work.

JUNCACEAE

Rush Family

Perennial or annual grasslike herbs; stems terete or flattened, not jointed, caespitose or arising singly or few together from rhizomes; leaves sheathing, alternate or all basal, mostly 2–ranked, blades linear, sometimes much reduced or lacking; inflorescence headlike to open paniculate, subtended by an involucral bract; branches, heads, and pedicels often subtended by bractlets; flowers bisexual (ours), sometimes subtended by bracteoles borne at pedicel apices, directly below perianth; perianth much reduced, petals and sepals hardly if at all different and referred to herein as tepals, tepals membranous, rather scalelike, greenish or brownish, 6, an outer and inner set with 3 each; stamens (3) 6; pistal 1; ovary superior, with 1 or 3 chambers; fruit a capsule with 1 or 3 chambers.

11(1). Seeds numerous in each capsule; leaves glabrous, sheaths open; bracteoles subtending flowers entire or lacking .... *Juncus*

— Seeds 3 per capsule; leaf blades pubescent at least on margins near base except sometimes in *L. parviflora*, sheaths closed; bracteoles subtending flowers entire to lacerate .... *Luzula*

JUNCUS L. RUSH

Juncus

Perennial or annual grasslike herbs; stems terete or flattened; leaf blades flat, strongly folded, or terete, when terete sometimes hollow with cross membranes at intervals (septate) or reduced to a bristle or lacking; flowers as described in family; seeds numerous, minute, usually apiculate or tailed.

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1. Plants annual 2

— Plants perennial 3

2(1). Plants 0.5–2 cm tall, subscapose; scapose stem with 1 flower; stamens 3; leaves not over 0.5 cm long .... *J. bryoides*

— Plants 2–30 cm tall, not scapose; inflorescence with 1–20 flowers; stamens 6; leaves 0.5–10 cm long .... *J. bufonius*

3(1). Flowers (1) 2–5 in solitary terminal head; leaves basal or nearly so, hollow, septate; plants densely tufted, without rhizomes, 3–19 cm tall, infrequent in Uinta Mountains .... *J. triglumis*

— Flowers either more numerous or not in a solitary terminal head or plants otherwise different from above 4

4(3). Stems with 0–2 (rarely more) leaf blades; blades borne on lower 1/5 of plant, not hollow, not septate, sheaths sometimes ending in a rudimentary bristle instead of a leaf blade; flowers not in heads but borne singly, each subtended by 2 hyaline bracteoles; rhizomes lacking or short and plants mostly caespitose except in *J. arcticus* 5

— Stems with 2 or more well-developed leafblades, at least uppermost blade borne above lower 1/3 of plant or else hollow and septate; flowers borne in 1 or more heads and not individually subtended by bracteoles; plants mostly with rhizomes (note: *J. compressus* and *J. gerardii* with leafy stems and solitary, bracteolate flowers are keyed both ways) 12

5(4). Leaves all reduced to bladeless sheaths, upper ones sometimes with a bristle-tip, this not over 5 mm long; inflorescence with 5–75 or more flowers; seed not tailed 6

— At least uppermost leaf of most stems with a well-developed leaf blade well over 10 mm long, or, if leaves all reduced to bladeless sheaths (*J. drummondii*), inflorescence with only 1–3 flowers and seeds tailed 7

6(5). Involucral bract about as long or longer than stem and inflorescence appearing at or below midlength of plant; stems seldom over 1 mm thick, somewhat tufted; plants of Uinta Mountains above 2,950 m, rather rare .. *J. filiformis*

— Involucral bract mostly shorter than stem and inflorescence appearing above midlength of plant; stems often over 1 mm thick, mostly arising singly or few together from robust dark rhizomes; plants widespread .... *J. arcticus*

7(5). Seeds tailed at each end, tails 1/2 as long to longer than body; inflorescence with 1–6 flowers; stem-leaves with blades lacking or reduced to a bristle or uppermost 1(2) with a well-developed blade; plants mostly found above 2,620 m. 8

— Seeds apiculate but not tailed; inflorescence with (1)6–50 or more flowers; some of lower stem-leaves commonly with well-developed blades; plants commonly found below and above 2,620 m 10

8(7). Stems with bladeless leaves, uppermost and often lower sheaths tipped with a bristle, this not over 1 cm long; tails of seeds equal to or longer than body; tepals 5–8 mm long; capsules blunt and more or less retuse, equal to or a little shorter than tepals ... *J. drummondii*

— Most of stems with a well-developed leafblade on at least uppermost sheath, lower sheaths often tipped with a bristle; tails of seeds equal to or shorter than body; tepals and capsules various 9

9(8). Capsules ovoid, retuse at apex; tepals 4–5 (5.5) mm long; anthers less than 1 mm long; filaments longer than anthers .... *J. hallii*

— Capsules oblong, pointed; tepals 5–8 mm long; anthers 1.5–2 mm long; filaments only about 0.3 mm long .... *J. parryi*

10(8). Tepals, at least outer ones, with incurved or hooded tips, rather obtuse, 1.5–2.5 mm long; uppermost leaf often borne above midlength of stem 13

— Tepals with acute to acuminate erect tips, 3–5 mm long; uppermost leaf borne on lower 1/3 of stem 11

11(10). Capsules retuse at apex, completely 3-loculed; panicles mostly less than 2 cm long; tepals with hyaline margins extending to apex of acute tip; plants montane, mostly above 2,380 m .... *J. confusus*

— Capsules blunt but not retuse, incompletely 3-loculed; panicles various but often over 2 cm long; at least outer tepals with hyaline margins not extending to acuminate or acuminate-attennuate tip; plants found mostly below 2,380 m .... *J. tenuis*

12(4). Flowers borne singly, each subtended by 2 bracteoles; pedicels sometimes also subtended by bractlets; tepals with incurved or hooded tips, 1.5–2.5 mm long 13

— Flowers borne in 1–many heads, not subtended immediately by bracteoles; pedicels usually subtended by bractlets; tepals, at least outer ones, with erect or spreading tips, as short or longer than above 14

13(12). Anthers about 3 times longer than filaments; capsule ellipsoid-ovoid, equal or slightly exceeding tepals; plants sometimes over 40 cm tall, known in Utah from a single collection from a hot spring in Salt Lake County .... *J. gerardii*

— Anthers scarsely longer than filaments; capsule globose-ovoid, distinctly exserted; plants 20–40 cm tall, known from flood plains of Green and Colorado rivers ...... *J. compressus*

14(12). Leaf blades flat or strongly folded and appearing flat at least toward base, not terete, not hollow; sheaths with hyaline margins; capsules not exserted beyond tepals 15

— Leaf blades terete and hollow, if only toward tip, then sheaths without hyaline margins and capsules conspicuously exerted beyond tepals 17

15(14). Leaves strongly folded, narrow edge oriented toward the flattened stem; scarious margins of sheaths extending well beyond juncture with stem, gradually tapering to inconspicuous auricles or auricles lacking; margins of blade more or less united beyond scarious margins . . . . *J. ensifolius*

— Leaf blades flat, flat surface oriented toward terete stem; scarious margins of sheaths not extending beyond juncture with stem 16

16(15). Seeds tailed, tails as long or longer than body; tepals granular-papillate on back; heads sometimes with more than 10 flowers; plants known from Duchesne, Wasatch, and Salt Lake counties . . . . *J. regellii*

— Seeds apiculate but not tailed; tepals smooth on back; heads with 3–10 flowers; plants widespread . . . . *J. longistylis*

17(14). Leaf blades folded to enrolled toward base, becoming terete and hollow distally; sheaths without hyaline margins; auricles lacking; capsules conspicuously exceeding tepals; seeds long-tailed; stamens 6; plants rare, from above timberline on Uinta Mountain . . . . *J. castaneus*

— Leaf blades terete and hollow from collar and outward, septate; scarious margins of sheaths projected into auricles; capsules not much if any longer than tepals and seeds not tailed or else stamens 3; plants widespread 18

18(17). Seeds tailed; stamens 3; capsules conspicuously exceeding tepals; plants known from one collection in Box Elder County . . . *J. tweedii*

— Seeds not tailed; stamens 6; capsules various; plants widespread 19

19(18). Capsules tapered almost from base into a mostly nondehiscent conspicuous stylar beak, often divergent in all directions in mature globose or hemispheric head; heads rarely solitary, greenish or light brown; tepals acuminate or acuminate-subulate; rhizomes sometimes swollen and tuberous at nodes; plants found mostly below 2,320 m 20

— Capsules rather abruptly narrowed above into a dehiscent short or inconspicuous stylar bank, ascending to slightly spreading in heads, or, if spreading in all directions, then heads solitary; heads light or deep brown to blackish-purple; rhizomes not as above; plants from above and below 2,320 m 21

20(19). Auricles 1.5–5 mm long; tepals 4–5 mm long, with rigid long-acuminate or subulate tips; mature heads 10–15 mm wide; capsules shorter or scarsely longer than tepals; stems to 6 mm thick . . . . *J. torreyi*

— Auricles 0.25–1 mm long; tepals 2.5–3.5 mm long, acuminate, tips not so rigid as above; mature heads 5–12 mm wide; capsules to ca 1 mm longer than tepals; stems 1–2 mm thick . . . . *J. nodosus*

21(19). Larger tepals 3–5 mm long or, if smaller, then inflorescence with 1 or rarely 2 heads, equal to or conspicuously exceeding capsules 20

— Tepals 1.5–2.8 mm long, shorter than capsules; inflorescence with (1)4–25 heads 21

20(19). Heads 1 or rarely 2, globose or nearly so, with 5–40 or more flowers; anthers 0.5–1 mm long, shorter than filaments; tepals purplish black . . . . *J. mertensianus*

— Heads (1)2–13, not or hardly globose, with 3–13 flowers; anthers 1–2 mm long, longer than filaments; tepals brown to purplish black . . . . *J. nevadensis*

21(19). Outer tepals obtuse, mostly longer than inner ones; branches of inflorescence stiffly erect; capsule rather abruptly rounded at tip; plants of low elevations and montane . . . . . . *J. alpinus*

— Outer tepals acute, about equal to or shorter than inner ones; capsules rather gradually tapering to tip; branches of inflorescence spreading to nearly divaricate; plants rather rare, apprently not montane . . . . *J. articulatus*

***Juncus alpinus* Vill.** Northern Rush. Perennial plants 3(5–40) cm tall; stems loosely tufted on creeping rhizomes, with 1–2 leaves mostly borne on lower 1/3 or 1/2; leaves mostly all bearing well-developed blades; scarious margins of sheaths prolonged into auricles, these 0.5–1 mm long; blades terete, hollow, sepatate, 1–1.5 mm in diameter; involucral bract 1–7(10) cm long, sometimes leaflike; inflorescence 0.8–8.5 cm long, rather openly branched, branches mostly erect or strongly ascending, with (1)3–25 small heads or headlike glomerals; heads 3–4(5) mm long, with 2–6 flowers; bractlets subtending branches and heads scarious; pedicels obsolete or less than 1 mm long; bracteoles lacking; tepals 1.5–2.5 mm long, brownish to dark purple, outer ones usually slightly longer than the usually more obtuse inner ones; stamens 6, filaments ca 0.5 mm long, anthers 0.25–0.5 mm long; styles with stigmas ca 1 mm long; capsules 1-chambered, 2.5–3 mm long, rather abruptly narrowed to a stylar beak to 0.25 mm long. Seeps, bogs, margins of lakes and ponds, and along streams, often on limestone or other basic substrates at 1,524 to 2,800 m in Box Elder, Daggett, Duchesne, Garfield, Kane, Uintah, and Wayne counties; Alaska to Newfoundland and south to Washington, Colorado, and Quebec; 21 (vi). Some specimens are rather difficult to distinguish from those of *J. articulatus*.

Juncus articulatus **L.** Jointed Rush. Perennial plants 17–36 cm tall; stems loosely to rather densely tufted, from short stout or prolonged rootstocks, with 2–4 leaves, upper leaf often on upper 1/2 to 3/4 of stem; mostly bearing well-developed blades, sheaths with scarious margins prolonged into auricles ca 1 mm long, blades 0.5–2 mm wide, terete, sepetate; involucral bract 1–3.7 cm long; inflorescence 1.5–7 cm long, openly branched, branches ascending to divaricate, with 4–25 small heads; heads with (2) 5–10 flowers; bractlets subtending branches and heads scarious; pedicels obsolete or less than 1 mm long; bracteoles lacking; tepals 2–2.8 mm long, mostly all acute, equal or inner ones slightly longer than outer ones, greenish or purplish with conspicuous scarious margins, often minutely granular scabrous on back; stamens 6, filaments ca 0.5 mm long, anthers 0.5–0.7 mm long; styles and stigmas ca 1 mm long; capsules 1–chambered, 2.8–3.8 mm long, gradually tapered to a stylar beak to 0.25 mm long; seeds 0.4–0.5 mm long, apiculate. Along streams, sand bars of rivers, around ponds, and in wet lowland meadows at 1,220 to 1,710 m in Grand, San Juan, Tooele, and Utah counties; British Columbia to Newfoundland and south to Arizona and West Virginia, and Eurasia; 5 (i).

Juncus arcticus **Willd.** Wiregrass [*J. balticus* Willd.; *J. balticus* var. *montanus* Engelm.; *J. balticus* var. *vallicola* Rydb.]. Perennial plants 20–105 cm tall; stems terete or slightly compressed, 1–5 mm in diameter, arising singly, 2–3 together, or rather tightly clustered, from robust dark brown or blackish rhizomes to 5 mm in diameter; leaves reduced to bladeless sheaths, sheaths confined to lower 1/5 of plant, entire or occasionally tipped with a tiny bristle; involucral bract (2.5) 4–23 cm long, appearing as a continuation of stem; inflorescence 0.5–15 cm long, congested and headlike with few (ca 5) flowers to open paniculate with up to 75 or more flowers; bractlets subtending branches and pedicels scarious; pedicels nearly obsolete or to 8 mm long; bracteoles subtending flowers ovate or nearly so, scarious; tepals 3.5–5 mm long, acute to acuminate, pale to dark brown, outer ones often a little longer, more sharply pointed and with darker margins than the usually more rounded, often broadly scarious-margined inner ones; stamens 6, filaments ca 0.5 mm long, anthers 1.4–2.1 mm long; styles and stigmas to ca 3 mm long; capsules 3–4 mm long; seeds ca 0.6–0.8 mm long. Margins of ponds and lakes, along streams and rivers, in alkaline to nonalkaline meadows, seeps, springs, marshes, and swamps at 925 to 2,590 (3,050) m in all Utah counties except Morgan; circumboreal, widespread in western North America, Eurasia; 150 (i). *Juncus arcticus* forms a highly variable complex. It seems best to await further monographic work for disposition of infraspecific taxa.

Juncus bryoides **F. J. Hermann** Minute Rush. [*J. kellogii* Engelm. in a broad sense]. Annual plants ca 0.5–2 cm tall; scapose stems capillary, 0.1–0.15 mm thick; leaves basal or nearly so, mostly less than 1/2 as long as stems, flat or channeled, with scarious margins, not over 1 mm wide; inflorescence of a solitary terminal flower, this subtended by mostly 2 scarious bracteoles; tepals 1.5–2 mm long, acute, about equal; stamens 3, filaments ca 0.4 mm long, anthers ca 0.2 mm long; capsules shorter than tepals; seeds 0.3–0.4 mm long, obscurely apiculate. Ponderosa pine, aspen, and mountain brush communities apparently mostly on moist or spring-fed sandy soil or sandstone or quartzite at 2,400 to 2,550 m in Daggett, Salt Lake, Sevier, and Uintah counties; California to western Colorado; 5 (0). This small plant is easily overlooked and is probably more widespread than few collections indicate.

Juncus bufonius **L.** Toad Rush. [*J. bufonius* var. *occidentalis* F. J. Herm.; *J. sphaerocarpus* misapplied]. Tufted annual plants, 2–30 cm tall, from few to numerous fibrous roots; stems few to many; leaves basal and cauline or all basal in small plants, some of basal ones bladeless, margins of sheaths hyaline but not projected into auricles, blades 0.2–1 mm wide, involute or channeled; involucral bract to 3.5 cm long, filiform and leaflike, or scarious, much reduced and hardly different from bracteoles in small plants; inflorescence 0.6–12 cm long, often 1/4–4/5 the height of plant, with 1–20 flowers; flowers borne singly and sometimes rather remote; bractlets of nodes scarious, often aristate; pedicels obsolete or less than 1 mm long; bracteoles subtending flowers scarious, usually ovate; tepals 3–6(8) mm, lanceolate, acute to acuminate, inner ones shorter than and not as pointed as outer; stamens 6, filaments 0.7–1 mm long, anthers 0.3–0.8 mm long; styles less than 1 mm long; capsules incompletely 3–loculed, 3–4 mm long, ca 1/2 as long to nearly equalling the tepals, subglobose to cylindric-ovoid; seeds 0.3–0.5 mm long, scarcely apiculate. Moist or wet soil of rocky drainages, ephemeral pools, along streams and rivers, margins of ponds and lakes, hanging gardens, and wet meadows, in many plant communities at 1,135 to 2,850 m in all Utah counties except Iron; cosmopolitan except in tropics and extreme Arctic; 93 (viii).

***Juncus castaneus* J. E. Sm.** Chestnut Rush. Perennial plants, stems arising singly or 2 together from slender, rather long rhizomes, 7–22 cm tall; leaves extending up to upper 1/3–4/5 of stem, sheaths without hyaline margins, auricles lacking, blades strongly folded below, becoming channeled toward middle, and terete, hollow, and septate toward tip; involucral bract 1.5–3.5 cm long, scarious and broadly expanded below, prolonged into an involute tip; inflorescence 1–7 cm long, of 1–4 compact heads, heads ca 5–10 flowered, bractlets subtending pedicels scarious like the involucral bract but not with a prolonged involute tip; pedicels 2–4 mm long; bracteoles subtending flowers lacking; tepals 4–7 mm long at anthesis, linear-lanceolate, acute or inner ones somewhat obtuse, chestnut-colored or purplish brown; stamens 6, about 1 mm shorter than tepals at late anthesis, filaments ca 3 mm long, anthers ca 1 mm long; styles ca 2–3 mm long; capsules 1–loculed, 6–10 mm long, elongate, well exceeding tepals, gradually tapering into a stylar beak ca 1 mm long; seeds 2.5–4 mm long, strongly tailed, tails longer than body. Wet alpine communities in Wasatch Plateau and Uinta Mountains in Sanpete and Summit counties; circumboreal and south in mountains of western North America to New Mexico; 2 (i). The leaf blades are folded toward base and are thus similar to those of *J. ensifolius*, but sheaths are without scarious margins that are so prominent in those of *J. ensifolius*.

***Juncus compressus* Jacq.** Caespitose perennial plants from thickened short rootstocks and fibrous roots, 20–40 (60) cm tall; leaves on lower 1/2 of or extending well up on stems, scarious margins of sheaths terminating in scarious aricles, blades 0.5–1.2 mm wide, more or less channeled; involucral bract 2–15 cm long, leaflike; inflorescence 3–15 cm long, congested to open paniculate, with ca 12–80 flowers, these borne singly; bractlets subtending branches of inflorescence similar to but smaller than involucral bract, or upper ones scarious and much reduced; pedicels obsolete or to 3 mm long; bracteoles of flowers scarious, rounded to broadly acute; tepals 1.5–2.2 mm long, slightly coriaceous and incurved at tip, especially outer set; stamens with filaments ca 1 mm long and anthers ca 0.5–0.7 mm long; styles ca 1 mm long; capsules 2–2.5 mm long, subglobose, obtuse, exceeding tepals; seeds ca 0.4 mm long, apiculate at both ends. Sand bars, mud flats, swamps, and riparian communities along flood plain of the Green and Colorado rivers at 1,220 to 1,675 mm in Daggett, Emery, Grand, and Uintah counties; Montana to Utah and east to Nova Scotia, and Eurasia, most likely introduced in western United States and probably in the East; 8 (i).

***Juncus confusus* Cov.** Densely caespitose, perennial plants from fibrous roots, 8–52 cm tall; leaves basal or borne on lower 1/4 of stems, upper 2–4 with well-developed blades, these 0.5–1.3 mm wide, mostly narrower than stems, channeled or involute, hyaline margins of sheaths projected into rounded auricles; involucral bract 1–13 cm long, less than 1 mm wide, slender, with a scarious decurrent auricle; inflorescence 0.8–2 cm long, with (1)3–40 flowers, congested but flowers born singly and not in heads; bractlets subtending pedicels scarious or lowest one similar to but much smaller than the involucral bract; pedicels nearly obsolete or to ca 2 mm long; bracteoles 2 or these subtended by additional smaller ones borne on the pedicel; tepals 3–5 mm long, elliptic-lanceolate or lanceolate, acute to broadly acute, with conspicuous hyaline margins extending to tip, about equal or inner set slightly shorter; stamens to ca 1.7 mm long, anthers 0.5–0.6 mm long; styles ca 1 mm long; capsules 3–loculed, 3–4 mm long, subequal to tepals, retuse at apex; body of seeds ca 0.4 mm long, more or less blunt at apex with a bent apiculate tip from one side. Ponderosa pine, aspen, lodgepole pine, Engelmann spruce, dry and wet meadow, and streamside-willow communities at (2,070) 2,340 to 3,110 m in Box Elder, Cache, Daggett, Duchesne, Garfield, Iron, Juab, Morgan, Salt Lake, Sanpete, Sevier, Summit, Uintah, Utah, Wasatch, and Washington counties; British Columbia to Saskatchewan and south to California and New Mexico; 50 (xv).

Juncus drummondii **E. Mey. in Ledeb.** Densely caespitose perennial plants from fibrous roots, 8–40 cm tall; stems terete; leaves mostly on lower 1/4 of stem, reduced to sheaths or uppermost sheath mostly with a bristle-tip (much reduced blade), this 1–10 mm long or rarely longer, upper sheath slightly bilobed and scarious at apex; involucral bract 1–4 cm long, shorter than or exceeding inflorescence by 2 cm, terete, with scarious decurrent auricles; inflorescence 0.8–2(3) cm long, with (1) 2–3 flowers, flowers borne separately on pedicels 1–15(20) mm long, pedicels often subtended by and partly enveloped in scarious bractlets, lowest bractlet sometimes similar to but shorter than involucral bract, each flower subtended by 2 scarious bracteoles 2–4 mm long, these rounded to broadly acute; tepals 5–8 mm long, equal or outer set slightly longer, narrowly acute; stamens ca 2 mm long, anthers ca 2–3 times longer than filaments; styles ca 2 mm long; capsules 3–loculed, 5–7 mm long, about as long or a little shorter than the sepals, retuse at tip; body of seeds ca 1.5–2 mm long, appendaged on both ends, appendages as long or slightly longer than body. Lodgepole pine, spruce-fir, wet and dry meadow, and alpine communities, in wet to dry rocky places at 2,940 to 3,475 m in Box Elder, Daggett, Duchesne, Garfield, Grand, Juab, Piute, Salt Lake, Sevier, Summit, Uintah, Utah, and Wasatch counties; Rocky Mountains from Alaska to New Mexico; 76 (iv).

Juncus ensifolius **Wikstr.** Swordleaf Rush. Perennial plants 21–72 cm tall; stems flattened, arising singly or loosely to rather densely tufted, from creeping rhizomes; leaves clustered on lower 1/2 of stems, but upper one usually borne near or above midlength of stem, strongly folded and flattened, narrow ventral edge facing stem, with broad scarious margins of sheaths extending onto blade, hardly if at all projected into auricles, blades more or less closed above scarious margin, partly to completely septate in closed portion; involucral bract much reduced to leaflike and up to 5 cm long, but shorter than inflorescence; inflorescence 1–17 cm long, with (2) 3–90 or perhaps more heads, heads light green to nearly black, with 4–25 flowers; bractlets subtending heads and pedicels scarious; pedicels to ca 1 mm long; bracteoles lacking; tepals 2.3–4 mm long, inner ones slightly shorter and slightly less pointed than the acute outer ones; stamens 3 or 6, filaments about equal to anthers, these 0.4–1.3 (1.5) mm long, styles 0.5–1.5 mm long; capsules 3–loculed, rounded toward tip, equal or a little longer than tepals, body of seeds 0.4–0.6 mm long, with or without tailed appendages to 0.2 mm long at either end. There are three varieties as follows:

1. Stamens 3; plants rare in Utah .... *J. ensifolius* var. *ensifolius*
— Stamens 6; plants common 2
2. Heads (5) 10–60 (90) or perhaps more, mostly 3–8 mm thick, with ca 4–12 flowers; seeds with apiculate tails, or tails rarely lacking (in Utah specimens); plants common in Canyonlands section of the state, and wholly intergrading into the following variety throughout much of state .... *J. ensifolius* var. *brunnescens*
— Heads 2–10 or rarely more, mostly 8–15 mm thick, with ca 10–15(25) flowers; seeds with or without apiculate tails; plants state wide and over a wide elevational range, but more common in mountains and in Great Basin than preceding variety .... *J. ensifolius* var. *montanus*

Var. *brunnescens* (Rydb.) Cronq. [*J. brunnescens* Rydb.; *J. saximontanus* f. *brunnescens* (Rydb) F.J. Hermann; *J. tracyi* f. *utahensis* (R. F. Martin) F. J. Hermann; *J. utahensis* R. F. Martin]. Along rivers, streams, ditch banks, around seeps, springs, ponds, lakes, and in hanging gardens, marshes, meadows, and bogs at 1,065 to 2,450 (2,740) m in Beaver, Duchesne, Emery, Garfield, Grand, Iron, Kane, Rich, San Juan, Sanpete, Sevier, Summit, Uintah, Utah, Washington, and Wayne counties, and intergrading into var. *montanus* in nearly all counties of state; nearly throughout range of var. *montanus*, but more common southward especially in Arizona and the only phase in Texas; 145 (v). See discussion under var. *montanus*.

Var. *ensifolius* Wet places in mountains in Daggett, Salt Lake, Tooele, and Uintah counties; Alaska to northern Mexico and east to Alberta and Arizona, 4 (i). The few specimens from isolated stations in Utah with only 3 stamens per flower could be nothing more than odd specimens of var. *montanus*. However, to north of our area this is a common phase.

Var. *montanus* (Engelm.) C. L. Hitchc. [*J. xiphioides* var. *montanus* Engelm.; *J. saximontanus* A. Nels.; *J. tracyi* Rydb.]. In meadows, along streams and rivers, about seeps and springs and other wet places at (853) 1,830 to 3,100 m in all counties of state; Alaska to southern California and east to Saskatchewan and New Mexico; 128 (v). In the study of numerous specimens seen from the state, the following trends were noted: (1) Most plants of the lower elevations in the Canyonlands Section are rather easily assigned to var. *brunnescens*, and they mostly have apiculate-tailed seeds.(2) Plants of the Great Basin are often referrable to var. *montanus*, and they have apiculate but rarely tailed seeds, (3) Throughout the plateaus and mountains that run through the center of the state and in the Uinta Mountains, there are plants of both varieties and numerous intermediate plants, and seeds are commonly with or without tails in both varieties as well as in intermediate plants. Color phases of the inflorescence (pale green to purplish black) are also found in both varieties and in intermediate plants. Perhaps outside Utah the picture is somewhat clearer, but Utah seems to be near the center of where the two varieties overlap. More than 25% of the Utah specimens examined appeared to be intermediate.

***Juncus filiformis* L.** Plants perennial, 5–40 cm tall; stems arising singly or in tufts from creeping rhizomes, terete, rarely over 1 mm in diameter; leaves reduced to bladeless sheaths, uppermost one often tipped with a tiny bristle, confined to lower 1/5 of plant; involucral bract 10–27 cm long, appearing as a continuation of stem, as long or to over 4 times longer than stem; inflorescence appearing lateral and on lower 1/2 to 1/10 of plant, 0.5–1(2) cm long, compact, with ca 5–20 flowers, flowers borne singly; bractlets subtending branches and pedicels scarious, lower ones sometimes aristate; pedicels nearly obsolete or to 4 mm long; bracteoles scarious, ovate or oblong; tepals 3–4.5 mm long, greenish, lanceolate, acute to acuminate, subequal or outer ones slightly longer; stamens 6, filaments ca 0.6 mm, anthers 0.4–0.6 mm long; styles and stigmas less than 1 mm long; capsules 3–loculed, ca 2–3 mm long, greenish, ovoid to obovoid, abruptly tapered to a short stylar beak; seeds 0.4–0.6 mm long, minutely winged-apiculate at both ends. Wet subalpine meadows and along streams in Uinta Mountains at 2,990 to 3,200 m in Summit, Uintah, and Wasatch counties; Alaska to Labrador and south to Utah and West Virginia; 10 (iv).

***Juncus gerardii* Lois.** Black Grass; Mud Rush. Perennial plants 15–80 cm tall; stems somewhat tufted on slender dark rhizomes; leaves rather scattered on stems, upper ones usually borne on upper 1/2 of stem, lower ones bladeless or with reduced blades, upper blades flat, 1.5–3 mm wide; inflorescence with several to many flowers; flowers borne singly and subtended by scarious bracteoles, nearly sessile to long-pediceled; tepals 2–3.5 mm long, dark brown with a greenish midstripe, blunt and usually hooded at tip; stamens 6, anthers ca 1.5 mm long, ca 2–3 times longer than filaments; capsules ovoid to obovoid, rounded, about equaling but a little shorter than tepals; seeds 0.5–0.6 mm long, slightly apiculate at tapered end, nearly truncate-apiculate at other end. Becks Hot Spring in Salt Lake County (Flowers sn 24 Sept. 1924 UT). The population is not likely existing because the area is now part of Interstate 15; Eurasia, Atlantic and Pacific coasts in North America, and sporadic inland; 1(0).

***Juncus hallii* Engelm.** Halls Rush. Perennial caespitose plants 20–40 cm tall, from fibrous roots, rhizomes lacking; stems terete, to ca 1.5 mm thick; leaves basal and on lower 1/5 of plant, usually only uppermost cauline leaf bearing a well-developed blade, lower stem-leaves bladeless or tipped with a short bristle, innovations sometimes with well-developed blades; blades terete, upper side more or less channeled toward base, not or inconspicuously channeled toward tip, less than 1 mm wide; involucral bract 0.7–2.5 (7.5) cm long, scarious and caudate to awned, or elongate and leaflike, with scarious margins projected into auricles; inflorescence to 1.7 cm long, with (2) 3–6 flowers; flowers rather congested, but borne singly; bractlets subtending pedicels scarious, attenuate to caudate; pedicels 1–8 mm long; bracteoles subtending flowers hyaline, ovate to nearly orbicular; tepals 4–5(5.5) mm long, subequal or inner ones a little shorter, lanceolate, acute, usually with greenish centers flanked by purple and with hyaline margins; stamens 6, filaments 1–1.5 mm long, anthers 0.5–0.7 mm long; styles and stigmas not over 1 mm long; capsules 3–loculed, equaling or ca 1 mm longer than tepals, triquetrous, retuse at apex, dark brown to purplish black; body of seeds 0.6–0.7 mm long, tailed at each end, tails ca 1/2 as long as body. Dry, wet, and boggy meadows, margins of ponds and lakes, and along streams at 2,956 to 3,350 m in Beaver, Daggett, Duchesne, Garfield, Summit, Uintah, and Wasatch counties; Montana to Colorado and Utah; 13 (xi).

***Juncus longistylis* Torr. in Emory** Longstyle Rush. Perennial plants 20–63 cm tall; stems arising singly or few together from creeping rhizomes, terete; leaves somewhat crowded on lower 1/2 of stem, but uppermost one often on upper 1/2–3/4 of stem, scarious margins of sheaths prolonged into auricles to ca 1 mm long, blades flat, not hollow, not septate, 1–3 mm wide; involucral bract 1–4 cm long, about equaling or shorter than inflorescence, mostly scarious, rarely leaflike, narrowly attenuate to caudate; inflorescence 1–7.5 cm long, usually with (1) 3–13 heads, heads with 3–10 flowers; bractlets subtending heads and pedicels scarious, acute to caudate; pedicels to ca 2 mm long, concealed in scarious bractlets; tepals (4)5–6 mm long, acute to acuminate, often purplish with greenish center and broad whitish or silvery hyaline margins; stamens 6, filaments 0.5–1 mm long, anthers (1) 1.3–2 mm long; styles 1–2 mm long; stigmas ca 2 mm long; capsules 3–loculed, shorter than or rarely equaling tepals, rather abruptly tapered to or retuse at stylar beak, brownish or purplish black; seeds ca 0.5 mm long, apiculate at each end. Wet meadows, along streams and rivers, about seeps and springs and other wet places, occasionally in alkaline places at 1,380 to 3,350 m in Box Elder, Cache, Daggett, Duchesne, Emery, Garfield, Grand, Kane, Millard, Morgan, Salt Lake, San Juan, Sanpete, Sevier, Summit, Tooele, Uintah, Utah, Wasatch, and Wayne counties; southern Canada, Washington to South Dakota and south to California and New Mexico; 100 (viii).

***Juncus mertensianus* Bong.** Mertens Rush. Perennial plants 13–42 cm tall; stems arising singly or loosely to tightly clustered on long creeping or short rhizomes, rhizomes sometimes short and stout and plants caespitose with numerous fibrous roots; leaves basal and on upper 1/4–3/4 or higher on stems, scarious margins of sheaths projected into ligulelike auricles 0.5–2 mm long; blades terete, channeled above, hollow, septate, 0.5–2 mm wide when pressed; involucral bract 0.8–3.2 cm long, rarely leaflike, often caudate; inflorescence 0.5–1.5 (3.5) cm long, with 1 (2) head(s); heads with 5–40 or more flowers, to ca 1.5 cm thick; bractlets subtending heads and pedicels scarious, acute to caudate; pedicels to ca 1 mm long; bracteoles lacking; tepals 2.5–4 mm long, acute to acuminate, blackish purple; stamens 6, filaments 1–1.3 mm long, anthers 0.5–1 mm long, shorter than filaments; styles to 1 mm long; stigmas to 1 mm long; capsules 1–chambered, triquetrous, slightly to conspicuously shorter than tepals, abruptly tapered to or slightly retuse at stylar beak, often as blackish purple as tepals; seeds 0.5–0.7 mm long, apiculate but hardly tailed. Wet meadows, along streams, about seeps and springs, margins of lakes and ponds, and Engelmann spruce–lodgepole pine, and tundra communities at 2,435 to 3,415 m in Box Elder, Cache, Duchesne, Garfield, Iron, Juab, Piute, Salt Lake, San Juan, Sanpete, Sevier, Summit, Uintah, Utah, and Wasatch counties; Alaska and Yukon south to southern California and South Dakota; 83 (vi).

***Juncus nevadensis* Wats.** Nevada Rush. [*J. badius* Suksd.]. Perennial plants 12–35 (53) cm tall; stems more or less terete, arising singly or a few together from creeping rhizomes; leaves basal and on upper 1/4–3/4 or higher on stems, with well-developed blades, scarious margins of sheaths projected into ligulelike auricles 1.5–3 mm long, blades terete, hollow, septate, somewhat channeled above, 0.5–2 mm wide; involucral bract 1–3(8.5) cm long, bractlike to leaflike, seldom much exceeding inflorescence; inflorescence 1–8 cm long, with (1) 2–13 heads, heads with (3)6–13 or more flowers; bractlets subtending, heads membranous, attenuate to caudate; pedicels to ca 1 mm long; bracteoles lacking; tepals (3) 3.5–5 mm long, brown to purplish black; anthers 1–2 mm long, longer than filaments; styles to 3 mm long, stigmas 1–2 mm long; capsules 1–loculed, equal to or conspicuously shorter than tepals, triquetrous, rounded or rarely slightly retuse at apex; seeds 0.5–0.6 mm long, apiculate but not tailed. Dry meadow, wet meadow, silver sagebrush-meadow, and lodgepole pine communities at 2,286 to 3,050 m in Box Elder, Cache, Daggett, Duchesne, Emery, Garfield, Grand, Kane, Rich, Sanpete, Summit, Uintah, Wasatch, and Washington counties; southern British Columbia and Alberta south to California and New Mexico; 43 (xvii). The inflorescence is sometimes similar to those of *J. ensifolius* and *J. longistylis*, and plants of these taxa are sometimes confused. The leaves are different in each of these. Occasional plants with only 1 or 2 heads are rather easily mistaken for those of *J. mertensianus*.

***Juncus nodosus* L.** Jointed Rush. Perennial plants 17–58 cm tall; stems terete, 1–2 mm thick, arising singly to densely clustered on creeping rhizomes, rhizomes sometimes with small tuberlike segments; leaves usually extending well up stems, those of stem with well-developed blades, those of innovations often without blades, scarious margins of sheaths prolonged into short auricles 0.25–1.0 mm long, blades terete or channeled above, hollow, septate, 0.5–1.5 mm wide when pressed; involucral bract 2.5–12 cm long, more or less leaflike; inflorescence 1.5–7 cm long, congested or rather open, with 3–12 globose or nearly globose heads; heads sessile or pedunculate, with (5) 10–25 flowers, 5–12 mm wide, flowers widely spreading to divergent; bractlets subtending heads scarious, acute to cuspidate; pedicels to ca 1 mm long; tepals 2.5–3.5 mm long, subequal, acuminate, acuminate tips shorter than and not so rigid as in those of *J. torreyi*; stamens 6, filaments ca 0.8 mm long, anthers 0.6–0.8 mm long; styles to about 3 mm long, stigmas ca 1 mm long; capsules incompletely 3-loculed, to ca 1 mm longer than tepals, slender, gradually prolonged into a tardily dehiscent stylar beak, sharply triangular in cross section; seeds 0.4–0.5 mm long, apiculate. Wetlands along streams and rivers and in wet and boggy meadows at (1,250) 1,640 to 2,320 m in Cache, Duchesne, Garfield, Piute, Rich, Summit, Uintah, Washington, and Wayne counties; southern Canada and Northern United States, south in West to California and Texas; 36 (xiii).

***Juncus parryi* Engelm.** Parrys Rush. Perennial caespitose plants (10)15–30 cm tall, from fibrous roots, lacking rhizomes; stems terete, about 1 mm thick; leaves basal and borne on lower 1/5 of stems, usually only uppermost one with a well-developed blade, lower sheaths usually tipped with a bristle or much reduced blade, and uppermost one sometimes reduced on a few of the stems, scarious margins of sheaths barely prolonged into auricles less than 0.5 mm long; blades less than 1 mm thick, terete, channeled to strongly involute below, obscurely channeled above, not septate; involucral bract 1.5–6(9) cm long, leaflike, terete, more or less simulating a continuation of stem, often auriculate; inflorescence 0.7–2.2 cm long, with 1–4 flowers, flowers borne singly; bractlets subtending pedicels scarious, acute to caudate, or one of them often similar to involucral bract but smaller; pedicels 1–20 mm long, abaxial ones often much longer than adaxial; bracteoles subtending tepals ovate to lance-ovate, rounded to acute or acuminate-attenuate; tepals 5–8 mm long, inner ones to 1 mm shorter than outer and somewhat less pointed and more scarious; stamens 6, filaments ca 0.3 mm long, anthers 1.5–2 mm long; styles ca 1.5 mm long, stigmas to 3.5 mm long; capsules a little shorter to a little longer than tepals; body of seeds 0.6–0.7 mm long, with tails a little shorter than or to 0.1 mm longer than body. Engelmann spruce, lodgepole pine, meadow, and alpine communities, on wet to dry rocky ground, sometimes in rocky snowflush areas at 2,620 to 3,420 m in Cache, Duchesne, Iron, Juab, Salt Lake, Summit, Uintah, and Wasatch counties; British Columbia to Alberta and south to California and Utah; 50 (v).

***Juncus regelii* Buch.** Regels Rush. [*J. jonesii* Rydb.]. Perennial plants 10–60 cm tall; stems arising singly or few together from creeping rhizomes; leaves basal and extending well up on stems, scarious margins of sheaths prolonged into inconspicuous or short auricles; blades flat, 2–4 mm wide, neither hollow nor septate; involucral bract 1–4 cm long; inflorescence with 1–5 globose or hemispherical heads, heads 8–20 mm across; bractlets subtending heads scarious; bracteoles lacking; pedicels ca 1–2 mm long; tepals 4–6 mm long, papillose-roughened on back, with a greenish midstripe flanked by dark brown and with scarious margins, inner ones slightly shorter and slightly less pointed than outer ones; stamens 6, anthers 1–1.5 mm long, subequal to filaments; capsules 3-loculed subequal to tepals, oblong-ovoid, truncate to retuse; body of seeds about 0.5 mm long, tailed at each end, tails about as long or longer than body. Meadows and along streams at 2,750 to 3,060 m in Duchesne, Salt Lake, and Wasatch counties; southern Washington to northern California and east to Montana and Utah; 8 (i). Much like *J. longistylis* but distinct in tailed seeds and more or less marked by papillose-roughened tepals.

Juncus tenuis **Willd.** Poverty Rush. [*J. dudley* Wiegand; *J. interior* Wiegand; *J. tenuis* var. *dudleyi* (Wiegand) F. J. Hermann; *J. tenuis* var. *congestus* Engelm.] Perennial, caespitose plants 22–65 cm tall, with fibrous roots; rhizomes lacking; stems terete, to 1.8 mm wide; leaves basal and cauline, borne on lower 1/5 of plant, those of stem mostly with well-developed blades, some of the basal ones with blades reduced to bristles, scarious margins of sheaths projected into auricles to ca 0.75 mm long; blades flat but soon moderately to strongly involute, not hollow, not septate, to ca 2 mm wide; involucral bract 2–18 cm long, leaflike; inflorescence (0.7)1.5–8.5 cm long, congested to rather open, with (4) 10–50 or more flowers, flowers borne singly; bractlets subtending branches and pedicels scarious, caudate-acuminate or awned, or lower ones leaflike and similar to involucral bract; pedicels obsolete or to 5 mm long; bracteoles subtending tepals scarious, ovate to lanceolate, acute to caudate; tepals 4–5 mm long, subequal or outer ones a little longer than inner, outer ones narrowly acuminate or acuminate-attenuate with hyaline margins mostly not extending on to acuminate tip, inner ones mostly acute to slightly acuminate with hyaline margins often extending to tip; stamens 6, filaments 0.6–1 mm long, anthers 0.5–0.8 mm long; styles and stigmas ca 1.5 mm long; capsules imperfectly 3-loculed, 1–2 mm shorter than tepals, obtuse to truncate; body of seeds 0.3–0.4 mm long, with apiculate ends to about 0.1 mm long. Along streams, washes, ditchbanks, rivers, margins of ponds and reservoirs, about seeps and springs, and in meadows and hanging gardens at 1,135 to 2,380 m in Cache, Daggett, Duchesne, Garfield, Grand, Millard, Rich, San Juan, Uintah, Utah, Wasatch, Washington, and Wayne counties; widespread in North America and introduced in temperate regions elsewhere in world; 41 (iv). Three intergradient phases can be seen in our plants (var. *dudleyi* with cartilaginous, often yellow to brown auricles about 0.5 mm long; vars. *congestus* and *tenuis* with membranous, usually greenish or whitish auricles often over 0.5 mm long, the former with congested panicles mostly less than 3 cm long, the latter with open panicles mostly over 3 cm long). The morphological differences are minor at best, and the taxa are more or less sympatric. Variety *tenuis* does seem to be more common in the southern half of the state. (Perhaps the recognition of these varieties serves more to waste time than for any important purpose.)

Juncus torreyi **Cov.** Torreys Rush. Perennial plants (10) 20–80 (100) cm tall; stems terete, to 6 mm in diameter near base, arising singly or a few together from robust creeping rhizomes, rhizomes often with swollen tuberlike segments; leaves well distributed up stem, scarious margins of sheaths prolonged into auricles, (1.5) 2–5 mm long; blades terete sometimes channeled on upper side, hollow, septate, 1–3 mm thick; involucral bract 1.5–17 cm long, more or less leaflike; inflorescence 1.5–7 cm long, congested, with (1) 3–13 more or less globose and sometimes burlike heads, heads 6–15 mm across, with 10–50 or more flowers, flowers widely spreading, and some usually reflexed; pedicels short and hidden in compact heads; bracteoles lacking; tepals 4–5 mm long, or inner ones slightly shorter, long-acuminate and rigid at tip; stamens 6, filaments 0.7–1 mm long, anthers 0.5–0.8 mm long; styles ca 0.25 mm long, stigmas ca 1 mm long; capsules incompletely 3-loculed, slender, triquetrous, equal to or slightly longer than tepals, slender stylar beak tardily dehiscent; seeds 0.4–0.5 mm long, apiculate but not tailed. Along streams, rivers, washes, and ditchbanks, at margins of ponds and lakes, about seeps and springs, and in saline or alkaline moist to wet meadows, marshes, and swamps at 850 to 2,010 m in all Utah counties except Iron, Millard, Piute, Summit, and Wasatch; southern Canada to northern Mexico; 112 (iv).

Juncus triglumis **L.** Three flowered Rush. [*J. albescens* Fern.]. Perennial plants 4–19 cm tall, densely caespitose; leaves basal or on lower 1/4 of stems, those of stem with well-developed blades, scarious margins of sheaths projected into auricles to about 0.75 mm long; blades about 0.5 mm wide, hollow, sepatate; involucral bract 5–10 mm long, often purplish; inflorescence a solitary head, this 5–8 mm long, with (1)2–5 flowers; bractlets subtending pedicels similar to but somewhat smaller than involucral bract; pedicels to ca 1 mm long; tepals 3–4 mm long, acute, cream, yellowish, or greenish yellow, and often marked with purple; stamens 6, as long as tepals or ca 1 mm shorter, filaments to 2 mm long, anthers 0.5–0.8 mm long; stigmas and styles about 1 mm long; capsules shorter or about 1 mm longer than tepals, abruptly tapered to blunt or subtruncate at tip, blackish purple; trigonous-cylindric body of seeds ca 0.75–1 mm long, tailed at both ends, each tail ca 1/2 to as long as body, more or less flattened, scarious. Wet meadows and bogs at 2,800 to 3,810 m in Uinta Mountains in Daggett, Duchesne, Summit, and Uintah counties; circumboreal, south in Rocky Mountains to New Mexico; 10 (v). Utah plants are referable to var. *albescens* Lange.

Juncus tweedyi **Rydb.** [*J. canadensis* var. *kuntzei* Buchenau]. Perennial plants 20–40 cm tall, stems clustered, terete; rhizomes apparently lacking; leaves basal and cauline, scarious margins of sheath projected into auricles (0.5)1–2 mm long; blades 1–2.5 mm thick, terete or nearly so, hollow, septate; involucral bract shorter than or somewhat longer than inflorescence; inflorescence with 2–8 heads, these with 3–8 flowers, 3–8 mm wide, brown; bractlets subtending heads and pedicels scarious; bracteoles lacking; tepals 3–4 mm long gradually acute, inner ones equal to or a little longer than outer; stamens 3, anthers 0.5–0.7 mm long, shorter than filaments; capsule slightly longer than tepals, triquetrous, more or less acute, imperfectly 3–loculed; seeds cylindrical with tails ca 1 mm long at each end. Near Corinne in Box Elder County (Kuntze 3133, NY). Wet places about hot springs, Yellowstone National Park, Wyoming; 0 (0).

LUZULA DC. WOODRUSH

Perennial grasslike herbs generally with long spreading hairs along margins of leaf blades, at least when young; leaves sheathing, sheaths closed, blades flat; inflorescence headlike or spicate to open paniculate; flowers subtended by bracteoles; tepals 6; stamens 6; capsules 1–loculed, with 3 seeds, dehiscent along midribs of carples; seeds with or without caruncles, sometimes comose with extremely fine hairs.

1. Inflorescence an open panicle, panicle sometimes drooping; leaves glabrous or nearly so at maturity, blades 3–11 mm wide; plants 27–77 cm tall . . . . *L. parviflora*

— Inflorescence of few to several congested or remote spikes or spikelike racemes, sometimes headlike; margins of leaves pubescent with long hairs especially near collar, 1–6 mm wide; plants 5–42 cm tall 2

2. Flowers borne in a terminal compound spikelike or headlike inflorescence; leaves 1–3 mm wide; seeds without or with an inconspicuous caruncle; plants widespread . . . . *L. spicata*

— Inflorescence with 1 or more lateral spikes, some of laternal ones often borne on peduncles to 3(5.5) cm long; leaves 2–6 mm wide; seeds with a conspicuous caruncle; plants known from Uinta Mountains . . . . *L. campestris*

Luzula campestris **(L.) DC in Lam. & DC.** Hairy Woodrush. [*Juncus campestris* L.; *L. multiflora* (Retz.) Lej.; *L. intermedia* (Thuill.) A. Nels.] Plants 13–42 cm tall; stems more or less tufted; leaves basal and cauline, blades flat, 2–6 mm wide, margins with scattered to moderately dense villose hairs ca 2–7 mm long or longer; involucral bract 3–9 mm long, leaflike; some bractlets subtending branches and peduncles leaflike, others scarious; inflorescence 1.5–5 cm long, usually conspicuously branched, with 3–12 spikes; spikes 5–12 mm long, sessile or on peduncles to 3 (5.5) cm long, with 5–15 or more flowers; bracteoles subtending flowers hyaline, entire or ciliate to fringed; tepals 2–3.5 mm long, greenish to brownish, acute or acuminate to scarcely caudate; anthers ca 0.5–1 mm long, filaments about equal anthers; capsules equal to or shorter than tepals; seeds 1.4–1.7 mm long, with a whitish caruncle ca 0.3–0.6 mm long. Lodgepole pine, Engelmann spruce, and meadow communities at 2,440 to 3,110 m in Uinta Mountains in Daggett, Duchesne, Summit, Uintah, and Wasatch counties; widespread in temperate regions of world; 10 (vii). Utah plants apparently belong to var. *multiflora* (Ehrh.) Celak.

Luzula parviflora **(Ehrh.) Desv.** Millet Woodrush. [*Juncus parviflorus* Ehrh.; *L. wahlenbergii* Rupr. misapplied] Plants 27–77 cm tall; stems solitary or few together from short rhizomes and fibrous roots; leaves basal and cauline, glabrous or with a few scattered long-villose hairs especially near collar, blades flat, 2–11 mm wide; involucral bract scarious and as short as 1 cm or leaflike and to 4(7) cm long, shorter than inflorescence, sometimes sheathing at base for up to 1 cm; inflorescence 3.5–16 cm long, open-paniculate, with slender flexuous branches; bractlets subtending branches mostly scarious, sometimes frimbriate toward apex; flowers borne singly on slender pedicels to 10 mm long or 2–3 together on short pedicels; bracteoles subtending flowers hyaline, ovate-acute, entire to incised; tepals 1.5–2.5 mm long, brownish and partly hyaline, acute to acuminate, subequal; anthers 0.3–0.4, filaments ca 0.5 mm long; capsules slightly longer than tepals, blackish purple, shiny; seeds 1.2 mm long, with obsolete or inconspicuous caruncles at each end. Ponderosa pine, aspen, lodgepole pine, spruce-fir, willow-streamside, and wet meadow communities at 2,300 to 3,475 m in Beaver, Box Elder, Carbon, Daggett, Duchesne, Garfield, Grand, Iron, Juab, Piute, Salt Lake, San Juan, Sanpete, Sevier, Summit, Uintah, and Wasatch counties; circumboreal, extending south in western North America to California and New Mexico; 84 (v).

Luzula spicata **(L.) DC.** Spike Woodrush. Plants 5–40 cm tall; stems more or less caespitose from fibrous roots, rhizomes apprently lacking; leaves basal and cauline, blades flat and 1–3 mm wide or involute and to only 0.5 mm wide, margins with scattered to moderately dense long-villose hairs; involucral bract 0.7–4 cm long, bractlike or occasionally leaflike, shorter than or equal to inflorescence or occasionally longer; inflorescence 1–3 cm long often nodding, of ca 4–10 or perhaps more sessile or subsessile heads or short spikes that are congested into a continuous or basally interrupted compound spike, individual heads or spikes with few to several flowers; bractlets subtending spikes or heads scarious and bractlike, or rarely leaflike; bractleoles subtending flowers scarious, fimbriate-ciliate, acuminate-caudate; tepals 2–3 mm long, dark brown or partly hyaline, acuminate or acuminate caudate, inner ones a little shorter than outer ones; anthers 0.3–0.5 mm long, ca 1/2 as long or equal to filaments; capsules a little shorter than tepals; seeds 1–1.3 mm long, caruncle obsolete or inconspicuous, not over 0.2 mm long. Lodgepole pine, spruce, fir, dry meadow, wet meadow, streamside-meadow, alpine tundra, and rarely aspen and oak–ponderosa pine communities, also in talus and fell fields at 2,470 to 3,810 m in Daggett, Duchesne, Grand, Juab, Piute, Salt Lake, San Juan, Summit, Tooele, and Uintah counties; circumboreal, south in western North America to California and Arizona; 65 (vi).

ADVERTISEMENT CALL VARIATION IN THE ARIZONA TREE FROG, *HYLA WRIGHTORUM* TAYLOR, 1938

Brian K. Sullivan[1]

ABSTRACT.—Advertisement call variation and male mating success was investigated in a population of the Arizona tree frog, *Hyla wrightorum*, from central Arizona. Dominant frequency of advertisement calls was significantly correlated (negatively) with male snout-vent length. Males found mating were not significantly larger than nonmating males, nor was there a significant correlation between sizes of males and females found in amplexus. These results are discussed in relation to Renaud's (1977) work with *H. wrightorum* and in light of recent work with anurans in general.

The Arizona tree frog (*Hyla wrightorum*) is primarily restricted to the Petran Montane Conifer Forest Biome (Brown and Lowe 1980) along the Mogollon Rim in central Arizona and extreme west central New Mexico, and in the Huachuca Mountains of southern Arizona (Stebbins 1966, Renaud 1977). Other than discussions of taxonomy, to date little has been published concerning this anuran. In his description Taylor (1938) placed *H. wrightorum* in the *H. eximia* species group; subsequently a number of authors have considered *H. wrightorum* as a subspecies of *H. regilla* (Jameson et al. 1966, Jameson and Richmond 1971) or as conspecific with *H. eximia* (Duellman 1970). However, Renaud (1977) documented that *H. eximia*, *H. regilla*, and *H. wrightorum* are distinct in their morphology (primarily size) and advertisement calls, and in light of their allopatric distributions warrant recognition as full species. Unfortunately Renaud's work remains unpublished and, hence, largely overlooked.

Here I present an analysis of advertisement call variation in a population of *H. wrightorum* from central Arizona. I compare my results with those of Renaud (1977) and hope to draw attention to his valuable work. I also examine the relationship between male size and mating success and test the hypothesis that advertisement call parameters (frequency, pulse rate, and duration) are predictably related to male snout-vent length.

MATERIALS AND METHODS

Breeding aggregations of *H. wrightorum* were observed near the towns of Pine and Strawberry along state route 87, Gila County, Arizona, on the night of 15 July 1984. A third population was observed breeding at Baker Lake near the intersection of forest route 300 and state route 87, Coconino County, Arizona, on the night of 21 July 1984. Calling males were recorded in the field using a Uher Recorder (4000 IC) and a Shure Unidyne IV (548) microphone. Immediately after recording a call, the cloacal temperature of the male was measured with a Schultheis Quick Recording Thermometer. Water and air temperatures were recorded at the calling site as well. All recorded males were collected and toe-clipped for permanent identification. A sample of amplexing pairs was collected at Baker Lake to test the prediction that large males were disproportionately successful in mating (Gatz 1981, Forester and Czarnowsky, 1985).

Calls were analyzed with a Kay 6061 B Sonagraph. Dominant frequency of advertisement calls was measured to the nearest 100 Hz from a section taken at call midpoint (Fig. 1). It is important to note that in *H. wrightorum* the advertisement call is somewhat frequency modulated, increasing about 400 Hz from the beginning to the end of a call. Rate of amplitude modulation was determined by counting the number of pulses in a 0.15-second portion of a wide-band (filter = 300 Hz) audio-spectrogram of three calls for each male, and averaged to yield a mean pulse rate. Similarly, call durations were measured in seconds directly from audio-spectrograms for three calls of each frog, and a mean duration was subsequently calculated.

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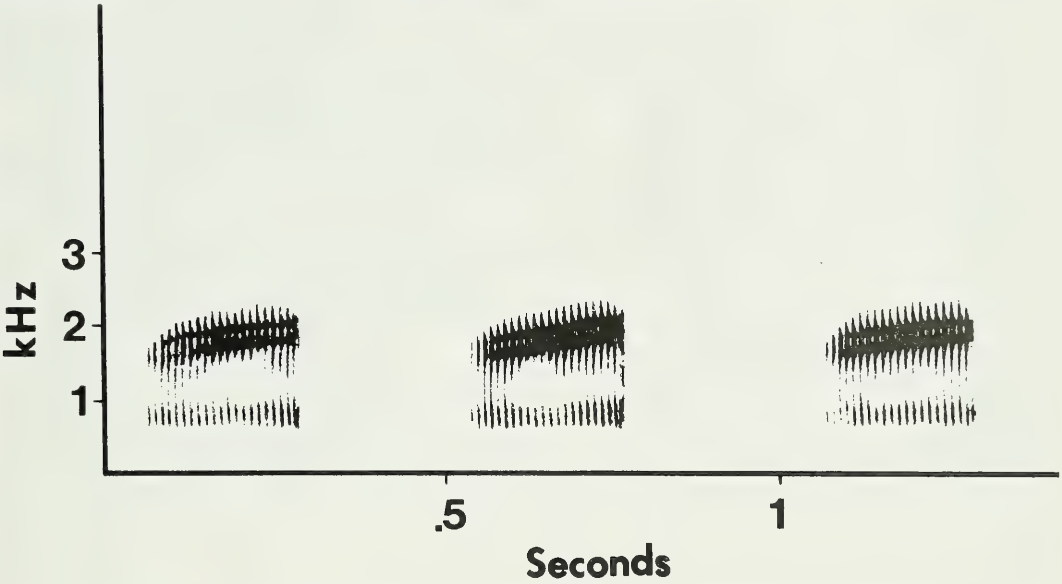

Fig. 1. Audio-spectrogram (filter = 300 Hz) of *Hyla wrightorum* advertisement call. Body temperature = 18 C, snout-vent length = 41 mm.

TABLE 1. Mean (x̄), standard deviation (SD) and extremes for advertisement call parameters, and snout-vent length of *Hyla wrightorum* from Baker Lake, Arizona (N = 20 for both samples).

	Present study			Renaud (1977)		
	x̄	SD	Extremes	x̄	SD	Extremes
Snout-vent length (mm)	41.30	2.48	37.00– 47.00	37.30	2.64	31.00– 45.00
Dominant frequency (kHz)	1.86	0.20	1.70– 2.30	1.93	0.19	1.60– 2.20
Pulse rate (p/s)	118.10	17.66	83.00–156.00	98.70	12.30	77.50–123.30
Call duration (s)	0.18	0.03	0.13– 0.24	0.17	0.02	0.12– 0.22

For analysis of variation in advertisement call parameters in relation to size, snout-vent length was measured to the nearest millimeter with a plastic rule. Product-moment correlations between male snout-vent length and each of the call variables were calculated.

RESULTS AND DISCUSSION

A sufficient sample (N = 20) of calls for analysis was obtained only at Baker Lake on 21 July 1984. All calling males had body temperatures of 18 ± 1 C: hence, temperature-induced variation was considered negligible. Further, Renaud (1977) found no correlation between temperature and advertisement call variation in *H. wrightorum*. Variation in dominant frequency, pulse rate, and duration of advertisement calls of *H. wrightorum* from Baker Lake was within the range of variation documented by Renaud (1977) for this species. Renaud (1977) also recorded calls of a population of *H. wrightorum* at Baker Lake (Table 1). There was no significant difference in mean frequency ($t = 1.11$, $P > 0.05$) or mean duration ($t = 1.24$, $P > 0.05$) of advertisement calls recorded by Renaud compared with those of the present study. However, there was a significant difference in mean pulse rate ($t = 3.93$, $P < 0.001$). Variation in pulse rate of anuran advertisement calls is typically attributed to variation in body temperature (e.g., Gerhardt 1982); hence, these results suggest that pulse rate may be influenced by body temperature, contrary to Renaud's (1977) assertion. Unfortunately, temperatures are unavailable for his Baker Lake recordings.

Only dominant frequency was significantly ($r = -0.47$, $P < 0.04$, $N = 20$) correlated with

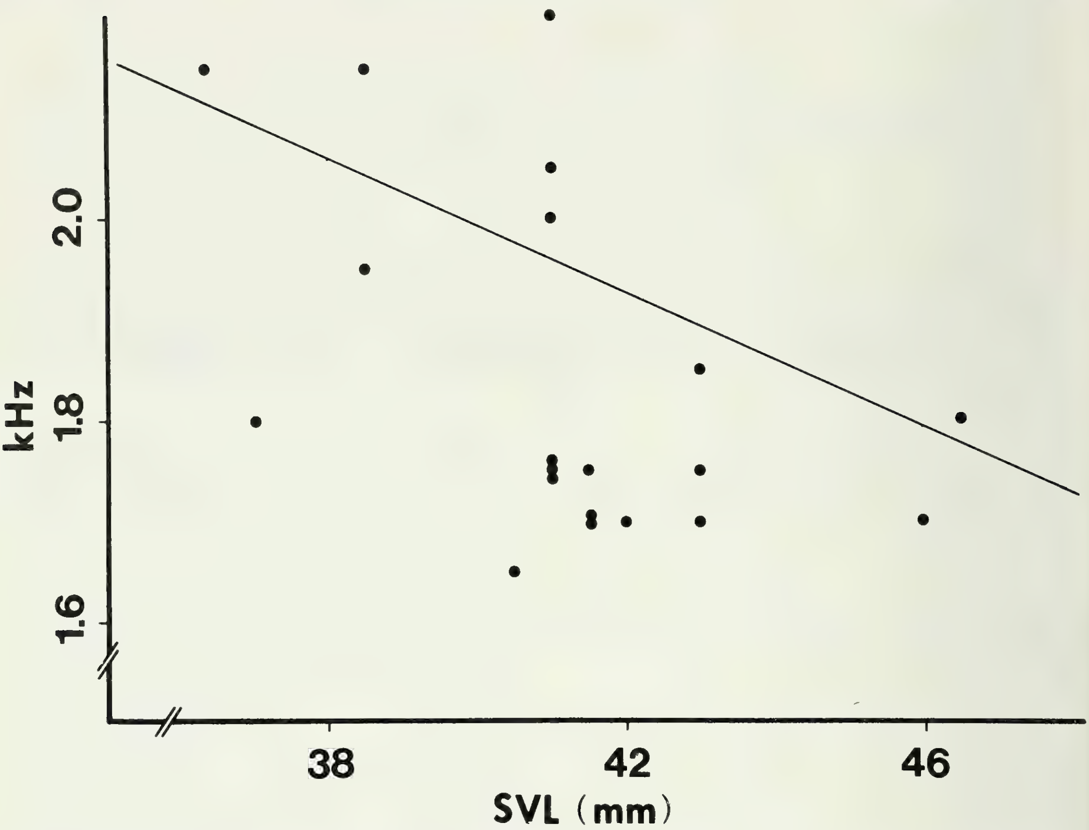

Fig. 2. Dominant frequency of advertisement calls against snout-vent length for 20 *Hyla wrightorum* from Baker Lake, Coconino County, Arizona. Body temperatures = 18 ± 1 C.

snout-vent length (Fig. 2). Neither pulse rate ($r = -0.24$, $P = 0.29$, $N = 20$) nor call duration ($r = 0.12$, $P = 0.60$, $N = 19$) were significantly correlated with male size. These results are consistent with a number of studies of anuran vocalizations and support the hypothesis that dominant frequency is determined by components of the vocal tract directly influenced by male body size (Martin 1972).

Many investigators of sexual selection in the Anura have documented a mating advantage for large males (see reviews by Kluge 1981, Gerhardt 1982). These workers have argued that females might select large mates on the basis of call parameters that are correlated with male snout-vent length. Such discrimination would be possible for *H. wrightorum* since advertisement call frequency is significantly correlated (negatively) with male size, presuming that females could detect small differences in frequency. However, males found in amplexus ($\bar{x} = 40.6$ mm snout-vent length) were not significantly ($t = 0.96$, $P > 0.30$, $N = 30$) larger than nonmating males ($\bar{x} = 41.3$ mm). Further, there was no correlation between the sizes of males and females in amplexus ($r = -0.04$, $P = 0.90$, $N = 10$). Hence, mating success of males appears unrelated to size, as has been documented for a number of other hylids (Fellers 1979, Gatz 1981, Kluge 1981, Gerhardt 1982, Forester and Czarnowsky 1985).

My results, as well as the more substantial work of Renaud (1977), reveal that advertisement calls of *H. wrightorum* are distinct from *H. eximia*. Calls of *H. wrightorum* have a higher pulse rate and shorter duration than the majority of Mexican *H. eximia* (Duellman 1970). It is hoped that this brief report will foster a reassessment of the taxonomic status of this Arizona anuran.

ACKNOWLEDGMENTS

This study was supported by the Department of Zoology at Arizona State University. Elizabeth Sullivan provided valuable field assistance.

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HE GREAT BASIN NATURALIST

lume 46 No. 3 31 July 1986 Brigham Young University

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10-86 650 25994

ISSN 017-3614

The Great Basin Naturalist
PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 46 31 July 1986 No. 3

NORTH AMERICAN STONEFLIES (PLECOPTERA): SYSTEMATICS, DISTRIBUTION, AND TAXONOMIC REFERENCES

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ABSTRACT.—A list of 537 Nearctic stonefly species is provided and distributions of all species are given by U.S. state and Canadian province. The list includes a bibliography of systematic and biogeographic papers published since the Zwick (1973) catalogue.

Periodically, it is useful to update catalog information on such well-studied groups as the nearctic Plecoptera. The most recent update by Baumann (1976) included distributions of genera by regions and reported a total of 470 nearctic species; prior to that list, the Illies (1966) and Zwick (1973) catalogs provided sources from which distributional data could be extracted. Unfortunately, not only are these works somewhat unavailable to workers, but also they are somewhat out of date. Consequently, we present this list of 537 species currently recognized (as of January 1986) from North America. Distribution records are reported by standard postal service abbreviation for U.S. states and Canadian provinces; Mexican records are given as MX, but only those species of nearctic origin are included because of the poor state of knowledge of the neotropical *Anacroneuria*. The list includes unpublished records provided by B. C. Kondratieff and R. F. Kirchner, along with a few from our personal collections, and the bibliography includes only those papers published since the Zwick (1973) catalog that contain new state or province records, or which reflect systematic changes for nearctic Plecoptera.

Since this list is likely to expand and undergo change as generic and specific limits are refined and phylogenetic affinities are postulated, we are maintaining the list in computer files. Currently we are using IBM and AT&T personal computers with Wordstar and WordPerfect software and a fortran program developed at Mississippi College for the HP 3000 mainframe academic computer. We suggest others with a vital interest in Plecoptera may also want to adopt this approach.

LIST OF ABBREVIATIONS

AB	Alberta	KS	Kansas
AL	Alabama	KY	Kentucky
AK	Alaska	LA	Louisiana
AR	Arkansas	LB	Labrador
AZ	Arizona	MA	Massachusetts
BC	British Columbia	MB	Manitoba
CA	California	MD	Maryland
CO	Colorado	ME	Maine
CT	Connecticut	MI	Michigan
DC	District of Columbia	MN	Minnesota
DE	Delaware	MO	Missouri
FL	Florida	MS	Mississippi
GA	Georgia	MT	Montana
IO	Iowa	MX	Mexico
ID	Idaho	NB	Nebraska
IL	Illinois	NC	North Carolina
IN	Indiana	ND	North Dakota

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NF	Newfoundland
NH	New Hampshire
NJ	New Jersey
NM	New Mexico
NS	Nova Scotia
NT	Northwest Territories
NV	Nevada
NW	New Brunswick
NY	New York
OH	Ohio
OK	Oklahoma
ON	Ontario
OR	Oregon
PA	Pennsylvania
QB	Quebec
RI	Rhode Island
SC	South Carolina
SD	South Dakota
SK	Saskatchewan
TN	Tennessee
TX	Texas
UT	Utah
VT	Vermont
VA	Virginia
WA	Washington
WI	Wisconsin
WV	West Virginia
WY	Wyoming
YK	Yukon

ACKNOWLEDGMENTS

We thank B. C. Kondratieff for reviewing an early draft of the list and L. C. Whitlock for his expertise in developing the HP 3000 program.

EUHOLOGNATHA

Capniidae

Capniinae

Allocapnia	
aurora Ricker	AL, DC, GA, MD, MS, NC, SC, TN, VA
brooksi Ross	TN
cunninghami Ross & Ricker	KY, TN
curiosa Frison	KY, MD, NY, PA, VA, WV
forbesi Frison	IL, IN, KY, OH, TN, WV
frisoni Ross & Ricker	KY, NY, OH, PA, TN, VA, WI, WV
frumi Kirchner	WV
fumosa Ross	NC, TN, VA
granulata (Claassen)	AL, AR, DC, IA, IL, IN, KS, KY, LA, MB, MD, MI, MN, MO, MS, NJ, NY, OH, OK, ON, PA, QB, TN, TX, VA, WI, WV
harperi Kirchner	VA, WV
illinoensis Frison	IL, IN, ME, MN, NY, OH, ON, QB, VA, WI
indianae Ricker	IN, KY, NY, OH
jeanae Ross	AR, OK
loshada Ricker	TN, VA, WV
malverna Ross	AR, LA, OK, TX
maria Hanson	CT, MA, MD, ME, NH, NS, NW, NY, PA, QB, VA, VT, WV
minima (Newport)	CT, IN, MA, ME, MI, MN, NF, NH, NS, NW, NY, ON, QB, VT, WI
mohri Ross & Ricker	AR, MO, OK
mystica Frison	AL, AR, GA, IL, IN, KY, MO, MS, OH, TN, VA, WV
nivicola (Fitch)	AL, CT, DC, DE, IL, IN, KY, MA, MD, NC, NJ, NS, NW, NY, OH, PA, QB, RI, TN, VA, VT, WI, WV
ohioensis Ross & Ricker	IN, KY, NY, OH, WV
ozarkana Ross	AR
pechumani Ross & Ricker	NW, NY, QB
peltoides Ross & Ricker	AR, OK
perplexa Ross & Ricker	TN
polemistis Ross & Ricker	AL
pygmaea (Burmeister)	CT, DC, IN, KY, MA, MD, ME, MI, MN, MO, NH, NS, NW, NY, ON, PA, QB, RI, TN, VA, VT, WI, WY
recta (Claassen)	AL, CT, DC, DE, GA, IL, IN, KY, MA, MD, ME, MS, NC, NH, NS, NY, OH, ON, PA, QB, SC, TN, VA, VT, WI, WV
rickeri Frison	AL, AR, DC, DE, GA, IA, IN, KS, KY, MD, MN, MO, MS, NC, NJ, NY, OH, OK, ON, PA, TN, VA, WI, WV
sandersoni Ricker	AR, MO, OK
simmonsi Kondratieff & Voshell	VA
smithi Ross & Ricker	AL, IL, KY, OH
stannardi Ross	NC, TN, VA
tennessa Ross & Ricker	AL, TN
unzickeri Ross & Yamamoto	TN
virginiana Frison	AL, DE, GA, MS, NC, SC, VA

vivipara (Claassen)	DC, IA, IL, IN, KS, KY, MD, MI, MN, MO, NY, OH, OK, ON, PA, QB, TN, VA, WI, WV
warreni Ross & Yamamoto	AR
wrayi Ross	DC, DE, GA, MD, NC, SC, TN, VA
zola Ricker	CT, KY, ME, NW, NY, OH, PA, TN, VA, WV

Bolshecapnia

gregsoni (Ricker)	BC
maculata (Jewett)	CA
milami (Nebeker & Gaufin)	AB, ID, MT
rogozera (Ricker)	BC
sasquatchi (Ricker)	AB, BC, MT
spenceri (Ricker)	AB, BC, MT

Capnia

bakeri (Banks)	CA
barbata Frison	AZ, CO, NM
barberi Claassen	CA
californica Claassen	AZ, CA
cheama Ricker	AB, BC, MT, YK
coloradensis Claassen	CO, ID, MB, MT, NM, SK, WY, YK
confusa Claassen	AB, AK, BC, CO, ID, MB, MT, NM, SK, UT, WY
cygna Jewett	ID, MT, UT, WA
decepta (Banks)	CO
disala Jewett	OR
elevata Frison	OR, WA
elongata Claassen	BC, CA, OR, WA
ensicala Jewett	OR, WA
erecta Jewett	OR
excavata Claassen	AK,BC,CA
fibula Claassen	AZ, NM
glabra Claassen	CA, OR
gracilaria Claassen	AB, BC, CA, CO, ID, MB, MT, NM, NV, OR, SK, UT, WY
hornigi Baumann & Sheldon	NV
jewetti Frison	OR
lacustra Jewett	CA, NV
licina Jewett	OR
lineata Hanson	CA, ID
manitoba Claassen	CT, MB, ME, QB, WI
melia Frison	AK, BC, OR
nana Claassen	AB, AK, BC, CO, ID, MT, OR, UT, WY
nearctica Banks	AK, BC, MB, NT, ON
nedia Nebeker & Gaufin	ID
oregona Frison	OR
petila Jewett	AB, ID, MT, OR, WY
pileata Jewett	BC, OR
promota Frison	BC, CA, OR, WA
quadrituberosa Hitchcock	CA
scobina Jewett	CA
sextuberculata Jewett	AB, MT, OR
spinulosa Claassen	CA
sugluka Ricker	QB
teresa Claassen	CA
tumida Claassen	BC, CA, OR
uintahi Gaufin	ID, NV, UT, WY
umpqua Frison	CA, OR
utahensis Gaufin & Jewett	NV, UT
venosa (Banks)	OR, WA
vernalis (Newport)	AB, BC, CO, ID, LB, MB, MN, MT, NM, OH, ON, QB, SK, UT, WI, WY
wanica Frison	CO, NM, NV, UT, WY
willametta Jewett	OR
zukeli Hanson	ID

Eucapnopsis

brevicauda Claassen	AB, AK, AZ, BC, CA, CO, ID, MT, NM, NV, OR, UT, WY

Isocapnia

abbreviata Frison	CA, OR
agassizi Ricker	BC, OR, WA
crinita (Needham & Claassen)	CO, ID, MT, SK, UT
fraseri Ricker	BC
grandis (Banks)	AB, AK, BC, CA, CO, MT, OR, UT
hyalita Ricker	CO, ID, MT, UT
integra Hanson	AB, MT
missouri Ricker	AB, ID, MT, SK, UT
mogila Ricker	OR
spenceri Ricker	BC, CA, OR
vedderensis (Ricker)	AB, BC, MT, NM, UT

Mesocapnia

arizonensis (Baumann & Gaufin)	AZ, NM
autumna (Baumann & Gaufin)	AK, BC, OR, WA
bergi (Ricker)	AK
frisoni (Baumann & Gaufin)	CO, NM, TX, UT
lapwae (Baumann & Gaufin)	CA, ID, OR
oenone (Neave)	AB, AK, BC, MT, OR, WA, YK
ogotoruka (Jewett)	AK
porrecta (Jewett)	CA, OR, WA
projecta (Frison)	BC, CA, OR, WA
variabilis (Klapalek)	AK, BC
werneri (Baumann & Gaufin)	AZ, CA, NM
yoloensis (Baumann & Gaufin)	CA, OR

Nemocapnia

carolina Banks	AL, AR, FL, IL, IN, MS, NC, QB, SC, VA

Paracapnia	
angulata Hanson	CO, CT, DE, IL, MA, MB, MD, ME, MI, NC, OH, OK, PA, QB, SK, TN, VA, WI, WV, WY
opis (Newman)	CT, ME, MN, NF, NY, ON, PA, QB, WI
oswegaptera (Jewett)	OR, WA
Utacapnia	
columbiana (Claassen)	AB, AK, BC, CA, MT, OR, YK
distincta (Frison)	AB, ID, MT, WY
imbera (Nebeker & Gaufin)	OR, WA
labradora (Ricker)	LB, QB
lemoniana (Nebeker & Gaufin)	CO, ID, NV, UT, WY
logana (Nebeker & Gaufin)	CO, NM, UT, WY
poda (Nebeker & Gaufin)	CO, MT, NM, UT, WY
sierra (Nebeker & Gaufin)	CA
tahoensis (Nebeker & Gaufin)	CA, NV
trava (Nebeker & Gaufin)	AB, ID, MB, MT, SK

Leuctridae

Leuctrinae

Despaxia	
augusta (Banks)	AK, BC, CA, ID, MT, OR, WA
Leuctra	
alabama James	AL
alexanderi Hanson	KY, NC, SC, TN, VA, WV
alta James	AL
baddecka Ricker	NS
biloba Claassen	AL, GA, NC, ON, TN, VA
carolinensis Claassen	NC, PA, SC, TN, VA
cottaquilla James	AL, FL, MS
crossi James	AL
duplicata Claassen	CT, ME, NY, ON, PA, QB, VA, WV
ferruginea (Walker)	AL, CT, DE, FL, IL, KY, MA, ME, MN, MS, NS, OH, PA, QB, SC, SK, VA, WI, WV
grandis Banks	MA, ME, NC, PA
laura Hitchcock	NH
maria Hanson	CT, NH, ON, QB, VT
mitchellensis Hanson	NC, VA
moha Ricker	AL, GA, SC
monticola Hanson	NC, SC, TN, VA
nephophila Hanson	NC, TN
rickeri James	AL, IL, KY, MS, OH
sibleyi Claassen	CT, DE, IL, IN, KY, MA, MD, ME, NC, NY, OH, ON, PA, QB, SC, TN, VA, WI, WV
szczytkoi Stark & Stewart	LA
tenella Provancher	CT, IN, LB, MA, ME, MN, MS, NJ, NS, NW, NY, ON, PA, QB, WI
tenuis (Pictet)	AL, AR, CT, DE, IL, MA, ME, MI, MN, MO, MS, NJ, NS, NY, OH, OK, ON, PA, QB, SC, TN, VA, WI, WV
triloba Claassen	FL, NC, NY, QB, SC, VA
truncata Claassen	CT, ME, NY, PA, QB, VA, WV
variabilis Hanson	MA, ME, NH, VA, VT
Moselia	
infuscata (Claassen)	BC, CA, NV, OR, WA
Paraleuctra	
andersoni Harper & Wildman	CA, OR
divisa (Hitchcock)	CA
forcipata (Frison)	AB, AK, BC, CA, ID, MT, OR
jewetti Nebeker & Gaufin	CO, MT, UT
occidentalis (Banks)	AB, AK, BC, CA, CO, ID, MT, NM, NV, OR, UT, WY
purcellana (Neave)	AB, BC, MT, OR, WY
rickeri Nebeker & Gaufin	AK, ID, MT, NM, UT
sara (Claassen)	CT, DE, KY, MA, ME, NC, NY, ON, QB, SC, TN, VA, WV
vershina Gaufin & Ricker	AB, AK, BC, CA, CO, ID, MT, NM, NV, OR, SK, UT, WA, WY
Perlomyia	
collaris Banks	BC, CA, ID, OR
utahensis Needham & Claassen	AB, BC, CA, CO, MT, NM, NV, OR, UT, WA, WY
Zealeuctra	
arnoldi Ricker & Ross	TX
cherokee Stark & Stewart	AR, OK
claasseni (Frison)	AR, IL, IN, KS, KY, MO, OK, TX, VA

fraxina Ricker & Ross	IL, KY, OH, TN, WV
hitei Ricker & Ross	TX
narfi Ricker & Ross	AR, IL, MO, OK, WI
warreni, Ricker & Ross	AR, MO, OK
washita Ricker & Ross	AR

Megaleuctrinae

Megaleuctra	
complicata Claassen	OR, WA
flinti Baumann	PA, VA
kincaidi Frison	ID, OR, WA
sierra Fields	CA
stigmata (Banks)	AB, BC, MB, MT, WA
williamsae Hanson	SC, TN, VA

Nemouridae

Amphinemurinae

Amphinemura	
apache Baumann & Gaufin	AZ
banksi Baumann & Gaufin	AZ, CO, ID, MT, SD, UT, WY
delosa (Ricker)	AL, AR, GA, IL, IN, KS, KY, MI, MO, MS, OH, OK, ON, PA, QB, TN, VA, WI, WV
linda (Ricker)	AB, AK, BC, CO, LB, MB, MI, NT, ON, PA, QB, SK, WI
mexicana Baumann	MX
mockfordi (Ricker)	TN
mogollonica Baumann & Gaufin	AZ, NM, UT
nigritta (Provancher)	AL, CT, DE, FL, GA, IL, IN, KY, LA, LB, ME, MS, NS, OH, PA, QB, SC, TN, TX, VA, WV
puebla Baumann	MX
reinerti Baumann	MX
varshava (Ricker)	IL, IN, KY, PA, WI
venusta (Banks)	AZ, MX
wui (Claassen)	CT, DE, GA, KY, MA, ME, NC, NJ, NS, NW, NY, PA, QB, SC, TN, VA, WV
Malenka	
bifurcata (Claassen)	OR, WA
biloba (Claassen)	CA
californica (Claassen)	AB, BC, CA, CO, ID, MB, MT, NV, SK, UT, WY
coloradensis (Banks)	AZ, CO, NM, SD, UT, WY
cornuta (Claassen)	BC, OR, WA
depressa (Banks)	CA, OR
flexura (Claassen)	AB, CO, ID, MT, NM, OR, WA, WY
marionae (Hitchcock)	CA
perplexa (Frison)	OR, WA
tina (Ricker)	ID, MT, NV, OR, WA
wenatchee (Ricker)	WA

Nemourinae

Lednia	
tumana (Ricker)	MT
Nemoura	
arctica Esben-Petersen	AB, AK, BC, MB, QB, SD
normani Ricker	AK, NT
rickeri Jewett	AK, MB, SK
spiniloba Jewett	CA
trispinosa Claassen	IL, LB, MB, ME, NS, NY, ON, QB, WI
Ostrocerca	
albidipennis (Walker)	CT, MA, ME, NH, NS, NY, ON, QB, VA
complexa (Claassen)	CT, MA, ME, NY, ON, PA, QB, VA, WV
dimicki (Frison)	BC, OR, WA
foersteri (Ricker)	BC, OR, WA
prolongata (Claassen)	DE, ME, NH, NW, QB, VA, WV
truncata (Claassen)	CT, MA, MD, ME, NY, OH, ON, PA, QB, VA, WV
Paranemoura	
perfecta (Walker)	CT, ME, NC, NS, NY, ON, PA, QB, VA, WV
Podmosta	
decepta (Frison)	AB, AK, BC, CO, ID, MT, OR, UT, WA
delicatula (Claassen)	AB, BC, CA, CO, ID, MT, NM, NV, OR, SK, UT, WY
macdunnoughi (Ricker)	LB, ME, NF, NS, QB
obscura (Frison)	OR, WA
weberi (Ricker)	AK, YK
Prostoia	
besametsa (Ricker)	AB, BC, CA, CO, ID, MT, NM, NV, OR, UT, WY
completa (Walker)	AL, AR, DE, IL, MA, ME, MI, MN, MO, MS, NC, NS, OK, ON, QB, SC, VA, WI, WV

hallasi Kondratieff & Kirchner	VA
similis (Hagen)	CT, DE, IN, KY, MA, ME, MI, MN, OH, QB, SC, VA, WI, WV

Shipsa

rotunda (Claassen)	AB, AK, AL, MB, MD, ME, MI, MN, NT, ON, QB, SC, SK, VA, WI

Soyedina

carolinensis (Claassen)	DE, NC, TN, VA, WV
interrupta (Claassen)	BC, OR, WA
nevadensis (Claassen)	CA, NV
potteri (Baumann & Gaufin)	ID, MT
producta (Claassen)	BC, CA, OR, WA
vallicularia (Wu)	CT, IN, KY, ME, MI, NS, NY, OH, ON, PA, QB, VA, WI, WV
washingtoni (Claassen)	CT, ME, NH, PA

Visoka

cataractae (Neave)	AB, BC, CA, ID, MT, OR, WA

Zapada

chila (Ricker)	TN
cinctipes (Banks)	AK, BC, CA, CO, ID, MB, MT, NM, NV, SD, SK, UT, WY
columbiana (Claassen)	AB, AK, BC, CA, ID, MT, OR, UT, WA, WY
cordillera (Baumann & Gaufin)	CA, ID, MT, OR, WA
frigida (Claassen)	AB, AK, BC, CA, CO, ID, MT, NM, NV, OR, UT, WA
glacier (Baumann & Gaufin)	MT
haysi (Ricker)	AB, AK, BC, CA, CO, ID, MT, NM, NV, OR, UT, WA, WY
oregonensis (Claassen)	AB, AK, BC, CA, CO, ID, MT, NV, OR, WY, YK
wahkeena (Jewett)	OR

Taeniopterygidae

Brachypteryinae

Bolotoperla

rossi (Frison)	ME, NC, NH, QB, VA, WV

Doddsia

occidentalis (Banks)	AK, BC, CA, CO, ID, MT, NM, NV, OR, UT, WA, WY

Oemopteryx

contorta (Needham & Claassen)	CT, KY, MA, ME, NH, TN, VA, WV
fosketti (Ricker)	AB, CO, MB, MT, SK, UT
glacialis (Newport)	CT, MN, NY, ON, QB, WI
vanduzeea (Claassen)	CA

Strophopteryx

appalachia Ricker & Ross	NC, TN, VA, WV
arkansae Ricker & Ross	AR, MO
cucullata Frison	OK
fasciata (Burmeister)	AL, CT, DE, IN, KS, KY, MB, ME, MN, MS, NC, ND, OH, OK, PA, QB, SC, WI
inaya Ricker & Ross	NC, SC
limata (Frison)	TN, VA
ostra Ricker & Ross	AR, OK, TX

Taenionema

atlanticum Ricker & Ross	CT, KY, LB, MA, MD, ME, NC, NF, NH, NY, QB, TN, VA, WV
californicum (Needham & Claassen)	CA
grinnelli (Banks)	CA
nigripenne (Banks)	AB, AZ, BC, CA, CO, ID, MT, NM, NV, OR, UT, WA, WY
oregonense (Needham & Claassen)	OR, WA
pacificum (Banks)	AB, AZ, BC, CA, CO, ID, MT, NM, OR, UT, WA, WY
pallidum (Banks)	BC, CA, CO, MT, NM, OR, UT, WA
raynorium (Claassen)	CA

Taeniopteryginae

Taeniopteryx

burksi Ricker & Ross	AL, CT, DE, FL, IA, IL, IN, KS, KY, LA, MD, ME, MN, MO, MS, OH, OK, ON, PA, QB, TN, TX, VA, WI, WV
lita Frison	AL, AR, FL, IL, IN, KY, LA, MS, NC, NJ, SC, TX, VA
lonicera Ricker & Ross	AL, FL, GA, LA, MD, MS, SC, TN, TX, VA

maura (Pictet)	AL, AR, CT, DE, GA, IN, KY, MA, MD, ME, MN, MS, NC, OH, PA, SC, TN, TX, VA, WV
metequi Ricker & Ross	AL, AR, IL, IN, KS, KY, OH, OK, ON, PA, VA, WV
nelsoni Kondratieff & Kirchner	VA
nivalis (Fitch)	AB, CA, CT, DE, ID, IL, IN, MB, ME, MN, NY, ON, OR, PA, QB, SK, UT, WI
parvula Banks	AB, AR, CT, GA, IN, KY, MB, ME, MI, MN, MS, NY, OH, ON, PA, QB, SC, TN, VA, WI, WV
pecos Baumann & Jacobi	NM
robinae Kondratieff & Kirchner	SC
starki Stewart & Szczytko	TX
ugola Ricker & Ross	GA, TN, VA, WV

SYSTELLOGNATHA

Chloroperlidae

Chloroperlinae

Alloperla	
acadiana Harper	NW
aracoma Harper & Kirchner	WV
atlantica Baumann	CT, GA, IN, MA, MD, ME, MI, MN, NC, NH, NS, NW, NY, ON, PA, QB, SC, TN, VA, VT
banksi Frison	IL, ME, MI, NS, NY, ON, VA
biserrata Nelson & Kondratieff	VA
caudata Frison	AR, CT, IL, IN, MA, ME, MO, NF, NS, OH, OK, QB, VA
chandleri Jewett	CA
chloris Frison	CT, KY, MA, ME, NY, OH, QB, VA, WV
concolor Ricker	CT, MA, ME, NF, ON, PA, QB, VA
delicata Frison	AB, BC, CA, ID, MT, OR
fraterna Frison	AK, BC, CA, OR, WA
furcula Surdick	SC
hamata Surdick	AL, AR, MO
idei (Ricker)	KY, ME, OH, QB, VA
imbecilla (Say)	IN, KY, NY, OH, QB, VA, WV
leonarda Ricker	ME, MI, MN, MO, QB
medveda Ricker	AB, BC, ID, MT, WY, YK
nanina Banks	GA, NC, NY, SC, TN, VA
natchez Surdick & Stark	MS
neglecta Frison	NC, NF, NY, ON, PA, TN, VA
ouachita Stark & Stewart	AR
pilosa Needham & Claassen	CO
roberti Surdick	IL
serrata Needham & Claassen	AB, AK, BC, ID, MT, WA, WY
severa (Hagen)	AB, AK, BC, CA, CO, ID, MT, NT, NV, OR, UT, WA, WY
usa Ricker	GA, SC, TN, VA, WV
voinae Ricker	MA, ME, NS, NY, QB, VT
vostoki Ricker	NS, NY, PA
Bisancora	
pastina (Jewett)	CA, OR
rutriformis Surdick	CA
Chloroperla	
ovibovis (Ricker)	AK, NT
Haploperla	
brevis (Banks)	AB, AL, AR, BC, CT, DE, GA, IL, IN, KY, MA, MB, MD, ME, MI, MN, MO, NC, NJ, NS, NW, NY, OH, OK, ON, PA, QB, SC, SK, TN, VA, WI, WV
chilnualna (Ricker)	BC, CA, OR, WA
chukcho (Surdick & Stark)	MS
orpha (Frison)	ME, MN, ND, NW, QB, WI
Neaviperla	
forcipata (Neave)	AB, AK, BC, MT, WA
Plumaperla	
diversa (Frison)	AB, AK, BC, CA, CO, ID, MT, NV, OR, UT, WA, YK
spinosa (Surdick)	CA
Rasvena	
terna (Frison)	NH, NY, TN, VT, WV
Suwallia	
autumna (Hoppe)	AB, BC, CA, ID, MT, OR, WA, WY
dubia (Frison)	AB, AK, BC, CO, ID, MT, OR, UT, WN, WY

lineosa (Banks)	BC, CO, ID, MT, OR, SK, UT, WA, WY
marginata (Banks)	LB, MA, ME, NY, PA, QB, VA, WV, WI
pallidula (Banks)	AB, AK, AZ, BC, CA, CO, ID, MB, MT, NM, NV, OR, UT, WA, WY

Sweltsa

albertensis (Needham & Claassen)	AB, ID, MT, WY
borealis (Banks)	AB, AK, BC, CA, CO, ID, MT, NM, NV, OR, SD, UT, WA, WY, YK
californica (Jewett)	CA
coloradensis (Banks)	AB, AZ, BC, CA, CO, ID, MT, NM, NV, OR, SD, UT, WA, WY
continua (Banks)	CA
exquisita (Frison)	AK, BC, OR, WA
fidelis (Banks)	AB, AK, BC, CA, CO, ID, NV, MT, OR, UT, WA, WY, YK
gaufini Baumann	ID, UT
hondo Baumann & Jacobi	NM
lamba (Needham & Claassen)	CO, ID, MT, NM, OR, UT, WY
lateralis (Banks)	CT, GA, MA, ME, NC, NH, PA, QB, SC, VA
mediana (Banks)	AL, CT, NC, PA, TN, VA
naica (Provancher)	IN, LB, ME, NS, NY, PA, QB, VA
occidens (Frison)	BC, ID, MT, OR, WA
onkos (Ricker)	DE, KY, LB, ME, NC, NS, NY, OH, ON, PA, QB, VA
oregonensis (Frison)	AK, BC, OR, WA
pacifica (Banks)	AK, BC, CA, ID, OR, WA
revelstoka (Jewett)	AB, BC, MT, OR, WA, WY
tamalpa (Ricker)	CA
townesi (Ricker)	CA, NV
urticae (Ricker)	NC, VA

Triznaka

pintada (Ricker)	AZ, CA, CO, ID, NM, NV, SD, UT, WA, WY
signata (Banks)	AK, BC, CO, ID, MT, NM, OR, SD, SK, UT, WA, WY

Paraperlinae

Kathroperla

perdita Banks	AB, BC, CA, ID, MT, NV, OR, WA

Paraperla

frontalis (Banks)	AB, AK, BC, CA, CO, ID, MT, NM, OR, SD, UT, WA, WY, YK
wilsoni Ricker	AB, BC, CA, ID, MT, OR, WA, YK

Utaperla

gaspesiana Harper & Roy	NH, PA, QB, WV
sopladora Ricker	AB, AK, BC, ID, MT, NV, UT, WY, YK

Peltoperlidae

Peltoperlinae

Peltoperla

arcuata Needham	KY, NY, PA, QB, TN, VA, WV

Sierraperla

cora (Needham & Smith)	CA, NV, OR

Soliperla

campanula (Jewett)	OR
fenderi (Jewett)	WA
quadrispinula (Jewett)	CA, OR
sierra Stark	CA
thyra (Needham & Smith)	CA, NV
tillamook Stark	OR

Tallaperla

anna (Needham & Smith)	GA, NC, PA, SC, VA,
cornelia (Needham & Smith)	FL, GA, NC, SC
elisa Stark	NC, TN
laurie (Ricker)	GA, SC, TN
lobata Stark	VA
maria (Needham & Smith)	CT, DE, GA, MA, MD, ME, NC, NH, NY, PA, SC, TN, VA, WV

Viehoperla

ada (Needham & Smith)	GA, NC, SC, TN

Yoraperla

brevis (Banks)	AB, BC, CA, ID, MT, NV, OR, WA, WY
mariana (Ricker)	BC, CA, OR, WA

Perlidae

Acroneuriinae

Acroneuriini

Acroneuria

abnormis (Newman)	AB, AL, CO, CT, DE, FL, GA, IA, IL, IN, KS, KY, LA, MA, MB,

	MD, ME, MI, MN, MS, MT, NB, NC, NM, NW, NY, OH, ON, PA, QB, SC, SK, TN, UT, VA, WI, WV, WY
arenosa (Pictet)	AL, DC, DE, FL, GA, LA,, MD, ME, MS, NJ, PA, QB, SC, TX, VA, WV
arida (Hagen)	GA, NC, NJ, PA, TN
carolinensis (Banks)	CT, KY, MA, MB, ME, MN, NC, NJ, NY, OH, ON, PA, QB, SC, TN, VA, WV
evoluta Klapalek	AR, IL, IN, KS, KY, MI, MO, OH, OK, ON, PA, TN, VA, WV
filicis Frison	AL, AR, GA, IL, IN, KY, MD, MO, OH, SC, TN, VA, WV
flinti Stark & Gaufin	VA
internata (Walker)	AR, GA, IL, IN, KY, MI, MN, MO, OK, VA, WI, WV
lycorias (Newman)	AB, CT, IL, KY, MB, ME, MI, MN, NY, OH, ON, PA, QB, SK, TN, VA, WI, WV
mela Frison	AL, AR, FL, GA, IL, IN, KS, MO, MS, OK, PA, TX
perplexa Frison	AL, AR, DC, GA, IL, IN, KY, MO, OH, OK, PA, TN, WV
petersi Stark & Gaufin	GA, TN
Attaneuria	
ruralis (Hagen)	AL, AR, DC, FL, GA, IA, IL, IN, KS, MB, MD, MN, MO, MS, NC, PA, SC, TN, VA, WI
Beloneuria	
georgiana (Banks)	GA, NC
jamesae Stark & Szczytko	AL
stewarti Stark & Szczytko	NC, SC, TN
Calineuria	
californica (Banks)	AB, BC, CA, ID, MT, OR, WA
Doroneuria	
baumanni Stark & Gaufin	BC, CA, NV, OR, WA
theodora (Needham & Claassen)	AB, BC, ID, MT, UT, WY

Eccoptura	
xanthenes (Newman)	AL, CT, DE, FL, GA, KY, MD, MS, NC, OH, PA, SC, TN, VA, WV
Hansonoperla	
appalachia Nelson	MA, TN, WV
Hesperoperla	
hoguei Baumann & Stark	CA
pacifica (Banks)	AB, AK, AZ, BC, CA, CO, ID, MT, NM, NV, OR, SD, SK, UT, WA, WY
Perlesta	
frisoni Banks	NC, SC, TN
placida (Hagen)	AL, AR, AZ, CT, DC, DE, FL, GA, IA, IL, IN, KS, KY, LA, MA, MB, ME, MO, MS, NB, OH, OK, ON, PA, QB, SC, SK, TN, TX, UT, VA, WI, WV, WY
Perlinella	
drymo (Newman)	AL, AR, CT, FL, IA, IL, IN, KS, KY, LA, MA, MD, ME, MI, MO, MS, NY, OH, OK, QB, SC, TX, VA, WI, WV
ephyre (Newman)	AL, AR, CT, FL, IN, KY, LA, MD, MN, MO, MS, NJ, OK, PA, SC, VA, WI, WV
fumipennis (Walsh)	AL, CT, FL, IL, MS, SC

Anacroneuriini

Anacroneuria	
wipukupa Baumann & Olson	AZ

Perlinae

Neoperlini

Neoperla	
carlsoni Stark & Baumann	FL, LA, MS, OK, SC, TX
catharae Stark & Baumann	AR, OH, VA
choctaw Stark & Baumann	OK, WV
clymene (Newman)	AL, CT, FL, GA, IN, KS, LA, MS, NY, OK, ON, PA, QB, TX, VA, WI, WV
freytagi Stark & Baumann	AR, KY, ME, NY, OH, ON, SC, TN, VA

gaufini Stark & Baumann	IN, KY, OH
mainensis Banks	ME, OH
stewarti Stark & Baumann	AR, KY, ME, MS, OH, VA, WI

Perlini

Agnetina	
capitata (Pictet)	CT, DC, DE, FL, GA, IN, KS, KY, LA, MA, MB, MD, ME, MN, MO, MS, NC, NH, NY, OH, OK, ON, PA, QB, SC, TN, VA, WI, WV
Claassenia	
sabulosa (Banks)	AB, AZ, BC, CA, CO, ID, MB, MT, NM, OR, QB, SD, SK, UT, WA, WY
Paragnetina	
fumosa (Banks)	AL, DC, FL, GA, LA, MS, NC, SC, TX, VA
ichusa Stark & Szczytko	NC, SC, TN
immarginata (Say)	CT, DE, GA, MA, ME, NC, NH, NY, PA, QB, SC, TN, VA, WV
kansensis (Banks)	AL, FL, GA, IL, IN, KS, LA, MS, SC
media (Walker)	CT, DE, IN, KY, MB, ME, MI, MO, NH, OH, ON, PA, QB, SK, VA, WI, WV

Perlodidae

Isoperlinae

Calliperla	
luctuosa (Banks)	CA, OR, WA
Cascadoperla	
trictura (Hoppe)	BC, CA, ID, MT, OR, WA
Clioperla	
clio (Newman)	AL, AR, CT, DE, FL, GA, IL, IN, KY, MA, MD, MI, MO, MS, NC, OH, OK, ON, PA, SC, TN, VA, WI, WV
Isoperla	
acula Jewett	CA
adunca Jewett	CA
baumanni Szczytko & Stewart	CA
bellona Banks	GA, NC
bifurcata Szczytko & Stewart	CA, ID, OR, WA
bilineata (Say)	CO, CT, IL, IN, KS, KY, MA, MB, ME, MI, MN, MS, NB, NC, NF, NW, NY, OH, ON, PA, QB, SK, VA, WI, WV
burksi Frison	AR, IL, IN, KY, OH, WV
conspicua Frison	IL
cotta Ricker	MA, MI, ON, QB, SC, WI, WV
coushatta Szczytko & Stewart	AR, DE, LA, MS, OK, TX, VA
davisi James	AL
decepta Frison	IL, IN, OH, ON
decolorata (Walker)	AK, BC, MB, NT, SK, YK
denningi Jewett	CA
dicala Frison	CT, FL, IN, MA, MB, ME, MI, MN, MO, ON, PA, QB, SC, TN, VA, WI, WV
distincta Nelson	NC, SC, TN
emarginata Harden & Mickel	MN
extensa Claassen	NB
francesca Harper	CT, MA, ME, NY, QB
frisoni Illies	BC, CT, DE, IN, MB, ME, MN, NS, NW, OH, QB, WI
fulva Claassen	AB, AZ, BC, CA, CO, ID, MT, NM, NV, OR, UT, WA, WY
fusca Needham & Claassen	AB, BC, ID, MT, OR, WA, WY, YK
gibbsae Harper	CT, NY, QB, WV
gravitans (Needham & Claassen)	OR, WA
holochlora (Klapalek)	CT, DE, GA, KY, MA, ME, NC, NY, PA, QB, SC, TN, VA, WV
irregularis (Klapalek)	TX
jewetti Szczytko & Stewart	CO, TX
katmaiensis Szczytko & Stewart	AK
lata Frison	MA, ME, MI, MN, NS, ON, QB, TN, VA, WI, WV
longiseta Banks	AB, BC, CO, IA, ID, IL, KS, MB, MN, MO, MT, NM, QB, SD, SK, UT, WI, WY
major Nelson & Kondratieff	VA
marlynia (Needham & Claassen)	IL, IN, KS, KY, MB, ME, MI, MN, NB, NH, NJ, NS, NW, OK, ON, PA, QB, SC, SK, VA, WI, WV

marmorata Needham & Claassen	CA, NV, OR, WA
maxana Harden & Mickel	MN
mohri Frison	AR, IL, KS, LA, MO, OK, PA
montana (Banks)	CT, DE, ME, MN, NH, NS, NY, ON, PA, QB
mormona Banks	AZ, BC, CA, CO, ID, MT, NM, OR, UT, WA, WY
namata Frison	AR, IN, KY, ME, MO, OH, PA, VA, WV
nana (Walsh)	IL, IN, KY, OH, ON, QB, WI
orata Frison	CT, FL, ME, MN, NC, NH, NS, NW, NY, OH, PA, QB, SC, TN, VA, VT, WV
ouachita Stark & Stewart	AR, OK
petersoni Needham & Christenson	AB, AK, BC, CO, ID, MT, SK, UT, WY, YK
phalerata (Smith)	CO, ID, NM, OR, SD, UT, WY
pinta Frison	AB, BC, CA, CO, ID, MT, OR, UT, WA, WY
quinquepunctata (Banks)	AB, BC, CA, CO, ID, MT, NM, NV, OR, SD, SK, UT, WY
raineri Jewett	OR, WA
richardsoni Frison	CT, IL, KY, MN, PA, WI, WV
roguensis Szczytko & Stewart	CA, OR
sagittata Szczytko & Stewart	TX
signata (Banks)	CT, MB, ME, MI, MN, NS, NW, NY, OH, OK, PA, QB, VA, WI, WV
similis (Hagen)	CT, DE, KY, MA, MD, ME, NC, NH, PA, QB, SC, TN, VA, WV
slossonae (Banks)	CT, ME, MI, MN, NH, NS, NW, NY, QB, VA, WI
sobria (Hagen)	AB, AK, AZ, BC, CA, CO, ID, MT, NM, NV, OR, UT, WA, WY, YK
sordida Banks	AB, BC, CA, ID, MT, OR, WA
tilasqua Szczytko & Stewart	OR
transmarina (Newman)	AB, BC, CT, DE, KY, LB, MB, ME, MI, MN, NF, NJ, NW, NY, ON, PA, QB, SK, VA, WI, WV

Perlodinae

Arcynopterygini

Arcynopteryx	
compacta (McLachlan)	AB, AK, BC, CO, ME, MT, NH, SK, WY
Frisonia	
picticeps (Hanson)	BC, CA, NV, OR, WA
Megarcys	
irregularis (Banks)	BC, WA
signata (Hagen)	AK, BC, CO, ID, MT, NM, NV, UT, WY
subtruncata Hanson	BC, ID, MT, OR, WA
watertoni (Ricker)	AB, BC, ID, MT
yosemite (Needham & Claassen)	CA, WA
Oroperla	
barbara Needham	CA
Perlinodes	
aurea (Smith)	AB, CA, ID, MT, OR, WA, WY
Setvena	
bradleyi (Smith)	AB, BC, ID, MT
tibialis (Banks)	BC, OR, WA
wahkeena Stewart & Stanger	OR
Skwala	
curvata (Hanson)	BC, ID, MT, OR, WA, WY
parallela (Frison)	AZ, BC, CA, CO, ID, MB, MT, NM, NV, OR, SK, UT, WA, WY

Diploperlini

Baumannella	
alameda (Needham & Claassen)	CA
Cultus	
aestivalis (Needham & Claassen)	AZ, BC, CO, ID, MT, NM, UT, WY, YK
decisus (Walker)	CT, GA, IN, KY, ME, MI, NC, NY, OH, ON, PA, QB, TN, VA, WV
pilatus (Frison)	BC, CA, ID, MT, OR, WA
tostonus (Ricker)	BC, CA, ID, MT, OR, WA, WY
Diploperla	
duplicata (Banks)	AL, DE, GA, MS, SC, TN, VA, WV
kanawholensis Kirchner & Kondratieff	WV
morgani Kondratieff & Voshell	VA, WV
robusta Stark & Gaufin	CT, IN, KY, OH, PA, VA, WV

Kogotus	
nonus (Needham & Claassen)	BC, CA, ID, MT, OR, WA, WY
modestus (Banks)	BC, CO, ID, MT, NM, UT, WY
Osobenus	
yakimae (Hoppe)	BC, CA, OR, WA
Pictetiella	
expansa (Banks)	CO, ID, MT, UT, WY
Remenus	
bilobatus (Needham & Claassen)	AL, CT, DE, GA, KY, NC, NY, PA, SC, TN, VA, WV
Rickera	
sorpta (Needham & Claassen)	CA, NV, OR, WA

Perlodini

Chernokrilus	
erratus (Claassen)	CA
misnomus (Claassen)	CA, OR
venustus (Jewett)	CA
Diura	
bicaudata (Linnaeus)	AK, MB, NT, SK, YK
knowltoni (Frison)	AB, BC, CA, CO, ID, MT, NM, NV, OR, SK, UT, WY, YK
nanseni (Kempny)	NH, QB
Helopicus	
bogaloosa Stark & Ray	FL, GA, LA, MS, SC
nalatus (Frison)	AR, IN, KS, MI, MO, OK
rickeri Stark	TN
subvarians (Banks)	CT, FL, KY, ME, NC, ON, PA, QB, SC, TN, VA, WV
Hydroperla	
crosbyi (Needham & Claassen)	AR, IL, IN, KS, MO, OK, TX
fugitans (Needham & Claassen)	AR, IL, IN, KS, TN, TX
phormidia Ray & Stark	FL, SC
Isogenoides	
colubrinus (Hagen)	AB, AK, AZ, BC, CA, CO, ID, MB, MT, NT, SK, UT, WY, YK
doratus (Frison)	IA, MI, PA, QB
elongatus (Hagen)	AB, AZ, BC, CO, ID, MB, MT, NM, UT, WA, WY
frontalis (Newman)	LB, MB, ME, MI, MN, NF, NY, QB, SK, WI
hansoni (Ricker)	CT, MA, MD, ME, NC, NS, NW, NY, PA, QB, VA, WV
krumholzi (Ricker)	MB, MI, MN
olivaceus (Walker)	MI, MN, ON, QB, WI
varians (Walsh)	IL, IN, MI, MN, MS, SC, TN
zionensis Hanson	AK, AZ, CO, NM, UT
Malirekus	
hastatus (Banks)	GA, KY, ME, NC, NY, QB, SC, TN, VA, VT, WV
Oconoperla	
innubila (Needham & Claassen)	NC, SC, TN
Yugus	
arinus (Frison)	GA, NC, PA, SC, TN, VA, WV
bulbosus (Frison)	GA, NC, PA, SC, TN, VA, WV

Pteronarcyidae

Pteronarcyinae

Pteronarcellini

Pteronarcella	
badia (Hagen)	AB, AK, AZ, BC, CO, ID, MT, NM, NV, OR, SK, UT, WY
regularis (Hagen)	AB, AK, CA, NV, OR, WA

Pteronacrcyini

Pteronarcys	
biloba Newman	AL, CT, GA, MA, ME, NC, NH, NS, NY, PA, QB, SC, VA, WV
californica Newport	AK, AZ, BC, CA, CO, ID, MT, NM, OR, UT, WA, WY
comstocki Smith	ME, NW, NY, PA, VA, WV
dorsata (Say)	AL, AB, AK, BC, FL, IL, KS, KY, LA, LB, MB, ME, MN, MS, MT, NB, NY, OH, PA, QB, SC, SK, TN, VA, WI, WV, WY
pictetii Hagen	CT, IL, IN, KS, KY, MB, MN, MO, OH, PA, TN, WI
princeps Banks	BC, CA, ID, NV, OR, UT
proteus Newman	KY, MB, ME, NC, NH, NY, PA, QB, SC, VA, WV
scotti Ricker	GA, NC, PA, SC, TN, VA

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THREE NEW RECORDS FOR DIATOMS FROM THE GREAT BASIN, USA

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Abstract.—Three diatom species recently collected from Great Basin localities represent new records of these taxa from this region of western North America. *Cocconeis scutellum* Ehr. and *Melosira dubia* Kuetz. were collected from a thermal spring in Tooele County, Utah. *Nitzschia hustedtiana* Salah was collected from newly flooded marshes at the south end of the Great Salt Lake, Tooele County, Utah.

We have recently studied the algal floras from several regions of western North America. In particular, during the past few years we have examined the algae from the Great Salt Lake (Felix and Rushforth 1977, 1979, 1980, Rushforth and Felix 1982) and several thermal systems in the Great Basin Desert (Kaczmarska and Rushforth 1983a, 1983b, St. Clair and Rushforth 1977). These systems have proven to contain taxa that are unusual in comparison to other habitats in the area. For instance, Blue Lake Warm Spring contains 41 taxa that were new records for the state of Utah, 17 of which were also new records for North America (Kaczmarska and Rushforth 1984).

As a part of ongoing ecological studies, we have examined the diatoms from a previously unstudied thermal system in Tooele County, Utah. We have also studied newly inundated marshlands created by the flooding of lands at the south end of the Great Salt Lake due to unusually high water during the past few years. While studying these samples, we encountered three taxa unusual in this region that represent or confirm new records for Utah. This paper is a report and discussion of these taxa.

Methods

Several periphyton samples were collected during 1983 and 1984 from a small thermal spring in Tooele County, Utah (T1S, R7W, Sec. 25), near the Genstar Dolomite Plant. These samples were collected by placing small amounts of attached algae and debris into vials. Similar samples were collected during July 1984 from ephemeral marshy pools at the south end of the Great Salt Lake, Tooele County, Utah (T2S, R4W, Sec. 4). All samples were returned to our laboratory and examined immediately. Samples were then cleared following standard procedures using boiling nitric acid. Strewn mounts were prepared using Naphrax high resolution mountant, and resulting slides were examined using Zeiss RA microscopes equipped with bright field and Nomarski optics.

Results and Discussion

The diatom floras of the two study sites were interesting in their floristic composition. At the Genstar locality, two of the dominant taxa were *Melosira dubia* Kuetz. and *Cocconeis scutellum* Ehr. *M. dubia* represents a new record for Utah, whereas *C. scutellum* confirms a single questioned report by Patrick (1936). Both of these taxa are typically coastal in distribution. The third taxon reported in the present paper, *Nitzschia hustedtiana* Salah, was collected from the Great Salt Lake locality. This diatom is similar to specimens previously reported as *Nitzschia punctata* (Wm. Smith) Grun. from Utah Lake, and *N.* species (Patrick 1936) from the Great Salt Lake. These three taxa are described and discussed below.

Cocconeis scutellum **Ehrenberg** 1838. Figs. 1–5, 8–9. Valve elliptical, 16–21 μm wide by 20–27 μm long; rapheless valve striae radiate, 8–10 in 10 μm, proliferating to 2–3 rows of small punctae near valve margin;

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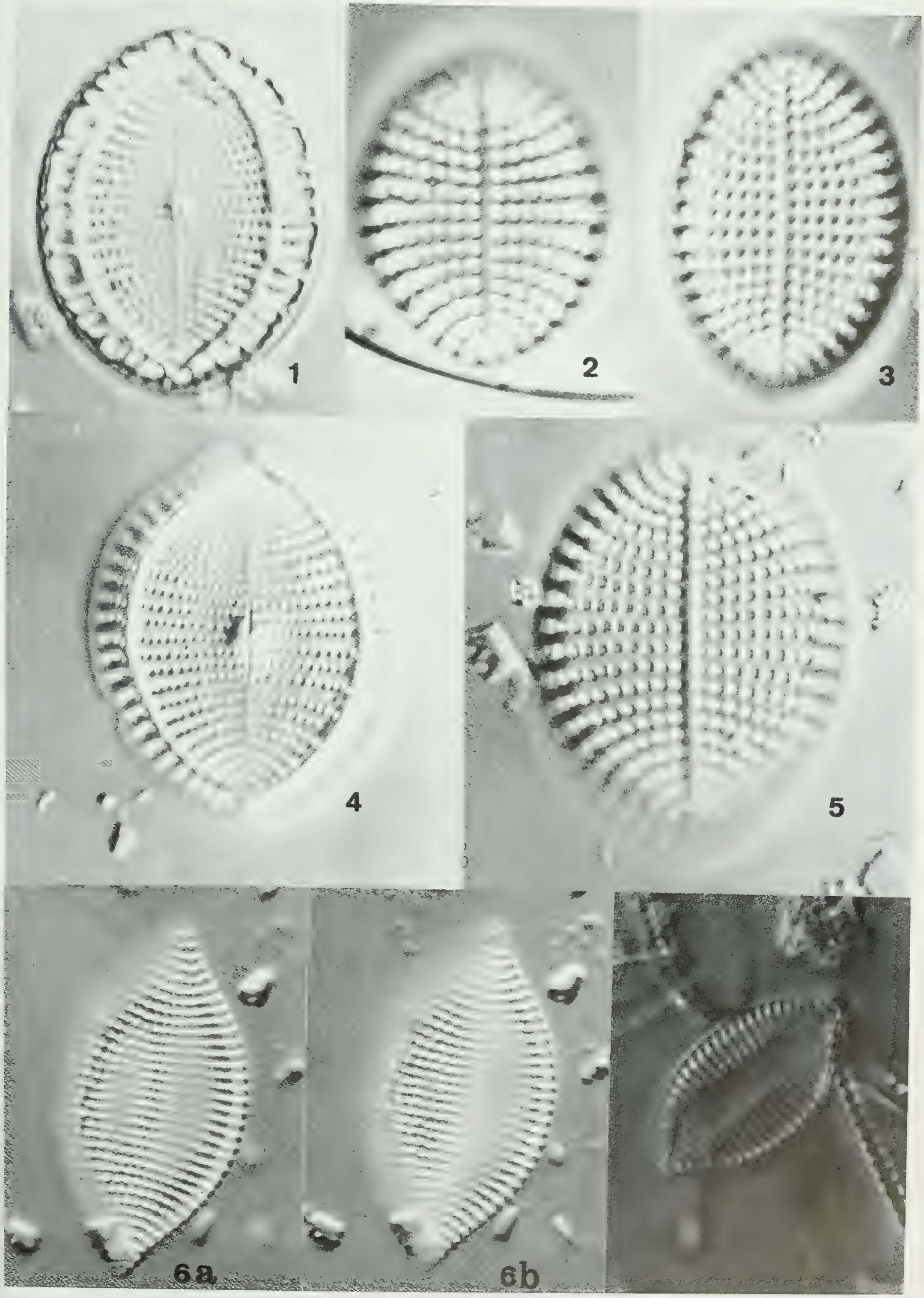
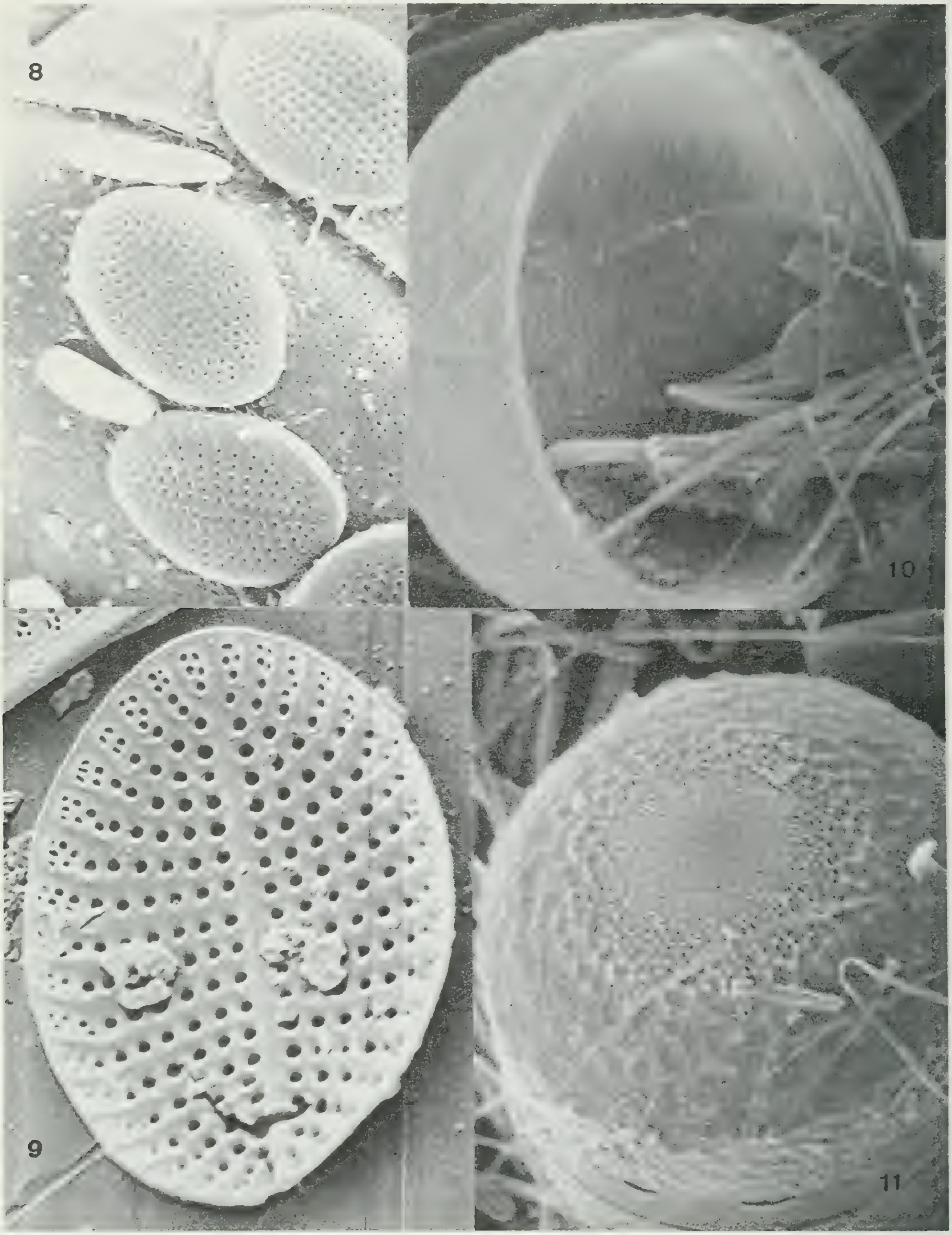
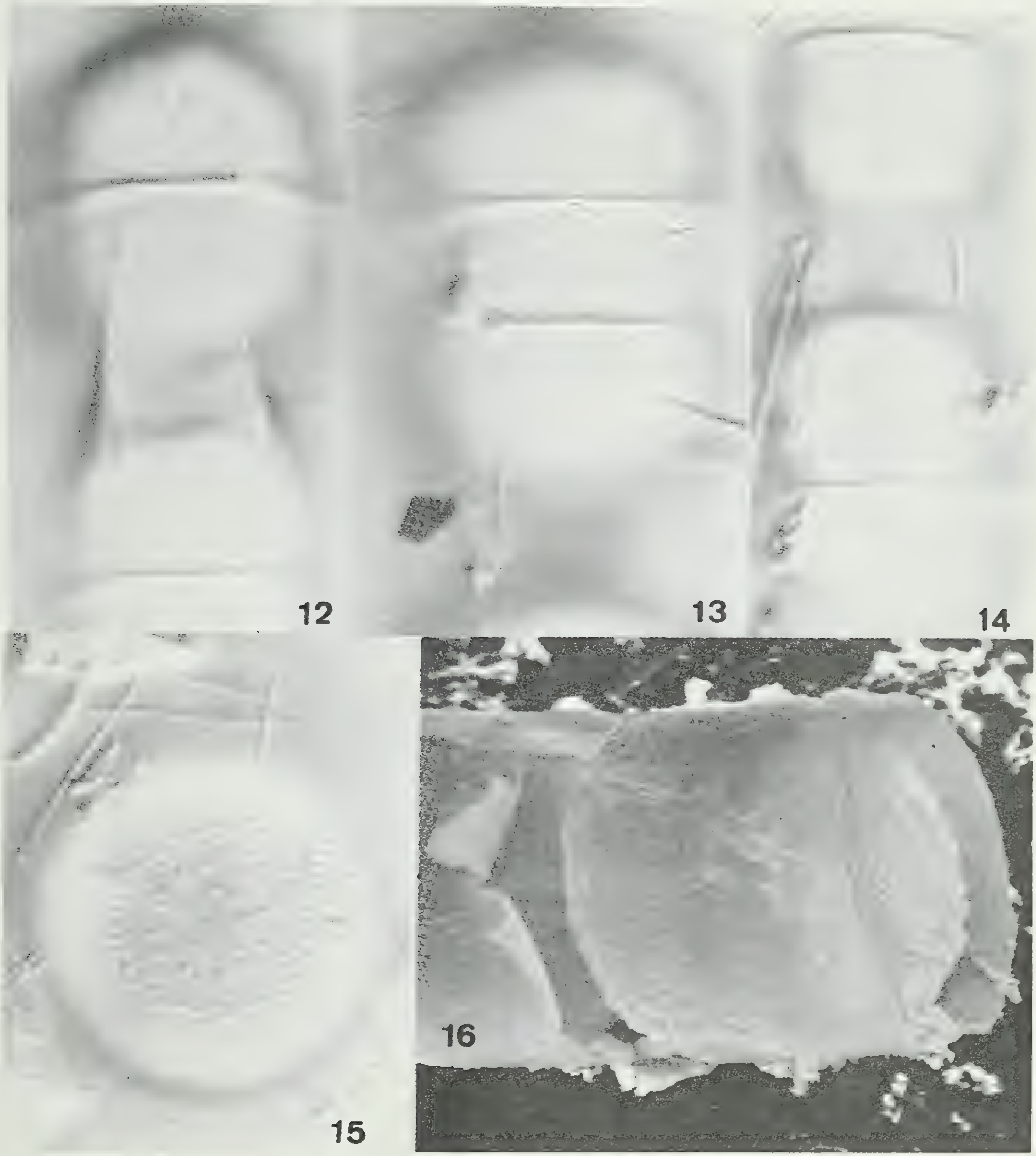


Figs. 1–7: 1,4, *Cocconeis scutellum* raphe valves, 2–3, 5, *Cocconeis scutellum* rapheless valves. 6–7, *Nitzschia hustedtiana*. All figures are X2000.



Figs. 8–11: 8, *Cocconeis scutellum* SEM of rapheless valve, X1600. 9, *Cocconeis scutellum* SEM of rapheless valve, X3700. 10, *Melosira dubia* SEM of inside of valve, X4250. 11, *Melosira dubia* SEM of valve surface, X4200.

punctae subquadrangular, aligned to form 10 longitudinal rows in 10 μm; axial area narrow, linear; raphe valve striae radiate, 10–13 in 10 μm, interrupted near margin by a hyaline ring; punctae round, 16–18 in 10 μm; raphe straight; axial area narrow; central area small,



Figs. 12–16. *Melosira dubia*: 12–14, Light micrographs of girdle views. 15, Light micrograph of valve view. 16, SEM of girdle view. All figures are X2000.

circular. Our specimens are small, although within the size range of 12–40 μm wide by 20–60 μm long given by Hustedt (1959) for *Cocconeis scutellum*. The striae are finer than those often reported for this species, and the raphe valve striae are finer than the rapheless valve striae. The fine striae are undoubtedly related to the small size of the valves, a characteristic also observed by Mizuno (1982), who found that striae density on both valves of *Cocconeis scutellum* var. *ornata* Grun. increased with decrease in valve length. His specimens also had finer striae on raphe valves than rapheless valves. *Cocconeis scutellum* occurred as an epiphyte on the green alga *Rhizoclonium* species and on the diatom *Pleurosira laevis* (Ehr.) Compére (= *Biddulphia laevis* Ehr.) in water with salinity approximately 5 0/00. It is a cosmopolitan polyhalobous species that is frequently reported from coastal regions.

Melosira dubia **Kuetzing**, 1844. Figs. 10–16. Cells cylindrical, 13–25 μm in diameter by 14–30 μm in height, attached to one another by mucilage pads to form chains often more than 15 cells long; valves convex, with a flattened apex and distinctive corona, lacking collars; valve surfaces warty, with several evident processes; striae generally not resolved in the light microscope. *Melosira dubia* is similar to *Melosira nummuloides*, *Melosira arctica*, and *Melosira moniliformis*. It differs from the former two especially in the absence of the collar on valve surfaces. It differs from *Melosira moniliformis* in several features, especially by being smaller and having an evident corona.

Nitzschia hustedtiana **Salah** 1952. Figs. 6–7. Valves elliptical to elliptical-lanceolate, with rostrate-apiculate ends, a longitudinal fold and indistinct keel, 6–13 μm wide by 15–24 μm long; striae 16–19 in 10 μm, nearly parallel near midvalve, strongly curved radiate near ends, distinctly punctate; punctae 16–20 in 10 μm. *Nitzschia hustedtiana* is similar to *Nitzschia punctata* (Wm. Smith) Grun., which is commonly reported from coastal areas. It differs by being smaller and having finer striation. In addition, the longitudinal fold and keel may be less distinct.

N. hustedtiana was discussed by Archibald (1983), who incorporated into this taxon other small *Nitzschia punctata*–like diatoms, including *Nitzschia punctata* f. *minores* Hustedt (1937–1938) and *Nitzschia subpunctata* Cholnoky (1960). Archibald also expanded the original size description of *Nitzschia hustedtiana* to 12.5–20.9 μm long by 5.5–8.0 μm wide based on collections from South African rivers. The Great Salt Lake specimens expand the size range of this taxon to 24 μm long and 13 μm wide, which intergrades with the size range of *Nitzschia punctata*. However, the striae density (16–19 in 10 μm) for *Nitzschia hustedtiana* is distinct from the 7–10 in 10 μm striae range typically reported for *Nitzschia punctata*.

A diatom described as *Nitzschia punctata* has been reported from Utah Lake phytoplankton (Rushforth et al. 1981, Rushforth and Squires 1985), bottom sediments (Grimes and Rushforth 1982), cores (Bolland 1974, Javakul and Rushforth 1983), and the stems of dead *Phragmites* plants on the shoreline (Grimes et al. 1980). These diatoms were 7–8 μm broad by 15–26 μm long, with 14–17 punctate striae in 10 μm and about 22 punctae in 10 μm. Utah Lake frustules differed from Great Salt Lake specimens by being linear-elliptical in shape, resembling closely the frustule illustrated by Cholnoky (1960) as *Nitzschia subpunctata*, which is now conspecific with *Nitzschia hustedtiana*. Thus, these Utah Lake specimens seem to be better identified as *Nitzschia hustedtiana* than *Nitzschia punctata*.

Nitzschia hustedtiana was rare in water with salinity approximately 56 0/00.

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MOVEMENTS BY SMALL MAMMALS ON A RADIOACTIVE WASTE DISPOSAL AREA IN SOUTHEASTERN IDAHO

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ABSTRACT.—Average linear movement by populations of *Dipodomys ordii*, *Microtus montanus*, *Perognathus parvus*, and *Peromyscus maniculatus* was investigated over a 15-month period by live trapping on a low-level, radioactive waste disposal area in Idaho. No significant differences in movement among habitats were observed seasonally, excepting *M. montanus* in spring. Average linear movements within habitats ranged from 20 to 70 m for all species, but some patterns varied seasonally and among age classes for individual species. Although predation on contaminated small mammals from the disposal area is a vector of radionuclide transport, local movements by these rodents do not appear to be of sufficient magnitude to contribute significantly to redistribution of radioactive particles.

The measurement of movements by small mammals has received considerable attention in ecological studies dealing with life history and estimation of density (Sanderson 1966). Recently several studies have focused on contamination of small mammals with chemical residues or radionuclides (e.g., Jefferies et al. 1973, Halford and Markham 1978), but only one investigation has considered movements by small mammals in the vicinity of a contaminated area (Hedlund and Rogers 1980). Preliminary studies on a radioactive waste disposal area in southeastern Idaho indicated that deer mice (*Peromyscus maniculatus*) tissues collected adjacent to the disposal area had higher concentrations of some radionuclides than tissues from control areas (Markham 1978, Markham et al. 1978). These data suggested that small mammals had access to contaminated soil areas near waste or were in direct contact with waste. Thus, small mammals could affect radionuclide distribution during their burrowing activities and move contaminated material in their gut, hide, or lungs.

On the basis of these observations, we undertook a study to examine the ecology and radioecology of small mammals inhabiting the waste disposal area. One objective of this study was to determine average linear movements by small mammals whose activity could affect the spread and redistribution of radionuclides, particularly via predation. The purpose of this paper is to report movements by small mammals on and adjacent to the disposal area and compare these movements among habitats and seasons and between sexes and age classes. Data on species diversity, biomass, population dynamics, and reproduction of small mammals on the disposal area (Groves and Keller 1983a), as well as radiation doses and radionuclide contamination to small mammals on the study area (Arthur et al. in press, 1986) have been reported previously.

METHODS

Our study was conducted at the Subsurface Disposal Area (SDA) of the Idaho National Engineering Laboratory (INEL) Radioactive Waste Management Complex. The INEL Site, a nuclear reactor testing facility under the jurisdiction of the U.S. Department of Energy, occupies 231,300 ha of sagebrush desert in southeastern Idaho. Since 1952 approximately 9.9×10^4 m^3 of radioactive wastes have been placed in pits and trenches at the SDA, a 36 ha portion of the complex used for disposal of radioactive waste. Details on the types of waste disposed at the SDA and waste disposal practices are provided in Arthur et al. (1986). Vegetation on the SDA was dominated by seeded crested wheatgrass (*Agropyron cristatum*), with Russian thistle (*Salsola kali*) growing over more recently disturbed and

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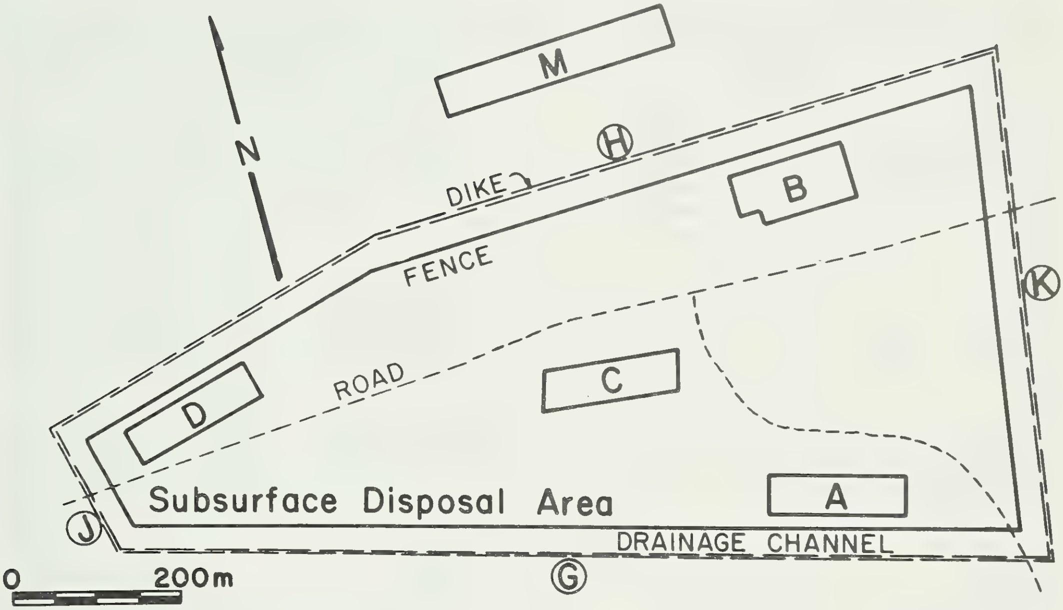

Fig. 1. Location of Grids A–D, M, and perimeter trap lines G, H, J, and K on and adjacent to the Subsurface Disposal Area.

unseeded areas. Native flora surrounding the disposal area is primarily big sagebrush (*Artemisia tridentata*)/bluebunch wheatgrass (*Agropyron spicatum*) steppe. Further details on the study area are provided in Groves and Keller (1983b).

Four trapping grids (A, B, C, D), each 0.6 ha and containing 100 Longworth live traps placed at 9 m intervals in a 5 x 20 configuration, were established on the SDA between May and July 1978 (Fig. 1). A fifth grid (M) was established in native vegetation 150 m north of the SDA during October 1978 and consisted of 160 live traps in a 5 x 32 configuration. On the perimeter of the SDA, a dry drainage channel lies between a dike and fence that surround the disposal area. Rodent populations in this area were studied by placing Longworth live traps at 9 m intervals around the entire perimeter (areas G, H, J, K).

Our study was conducted from May 1978 to July 1979. Perimeter lines and grids were trapped weekly on a staggered basis (i.e., grids on odd weeks, lines on even weeks) from May through October 1978, and monthly thereafter. A trapping session consisted of two days of trapping per grid or line. During this time traps were baited and set in late afternoon, followed by removal and examination of animals the following morning. Captured animals were eartagged with fingerling fish tags. Data obtained for each captured animal included species, trap location, weight, sex, and reproductive condition.

Three measures of movement (Brant 1962) were used to estimate movements by individual small mammals: (1) *D*, the average distance between captures from one trapping period to the next, (2) *M*, the maximum distance between captures from one trapping period to the next, and (3) *S*, average distance between captures within a two-day trapping session. *D* and *M* were employed to estimate how far an animal moved between trapping sessions, whereas *S* was used to estimate short-term movement, that is, movement from one day to the next within a trapping period. Following individual calculations, data were pooled to estimate average movement values for individual species.

Movement data were first separated into four seasonal periods: winter (December–February), spring (March–May), summer (June–August), and autumn (September–November). These periods corresponded well with changes in temperature and snowfall, as well as changes in population density and re-

TABLE 1. Seasonal estimates of the average distance (m) (±S.E. (n = number of animals)) between successive captures from one trapping period to the next (*D*) and within a trapping period (*S*) for *Peromyscus maniculatus* in different habitats on and adjacent to the Subsurface Disposal Area. Blanks in the table indicate sample size was less than or equal to five animals.

Habitat	Statistic	Winter	Spring	Summer	Autumn
Crested Wheatgrass	*D*	28.4 ± 5.2 (11)	25.5 ± 5.2 (46)	27.5 ± 3.8 (104)	23.8 ± 3.1 (83)
(A, B, D)	*S*	9.0 ± 2.8 (6)	16.2 ± 4.7 (35)	17.8 ± 4.0 (94)	33.7 ± 12.0 (73)
Russian Thistle	*D*	—	43.2 ± 18.1 (8)	45.1 ± 16.3 (20)	21.1 ± 3.2 (34)
(C)	*S*	—	—	16.4 ± 2.0 (15)	16.9 ± 4.1 (26)
Sagebrush	*D*	—	—	43.8 ± 7.0 (8)	—
(M)	*S*	—	—	19.6 ± 4.1 (6)	—
Fence line	*D*	21.1 ± 4.9 (50)	34.7 ± 4.7 (149)	36.8 ± 6.1 (195)	24.1 ± 4.5 (212)
(G, H, J, K)	*S*	14.4 ± 3.3 (33)	26.2 ± 5.3 (122)	20.6 ± 2.9 (165)	14.8 ± 2.4 (162)

TABLE 2. Seasonal estimates of the average distance (m) (±S.E. (n = number of animals)) between successive captures from one trapping period to the next (*D*) and within a trapping peroid (*S*) for *Dipodomys ordii* and *Microtus montanus* in different habitats on the Subsurface Disposal Area. The blank in the table indicates a sample size was less than five animals.

		Dipodomys ordii	
Habitat	Statistic	Summer	Autumn
Crested Wheatgrass	*D*	55.3 ± 25.5 (29)	37.5 ± 15.0 (30)
(A, B, D)	*S*	18.6 ± 3.8 (15)	22.3 ± 6.0 (25)
Fence line	*D*	51.2 ± 23.6 (38)	29.1 ± 5.1 (90)
(G, H, J, K)	*S*	33.2 ± 15.5 (30)	21.3 ± 5.9 (74)

		Microtus montanus	
Habitat	Statistic	Spring	Summer
Crested Wheatgrass	*D*	21.0 ± 3.1 (42)	68.4 ± 22.3 (16)
(A, B, D)	*S*	14.5 ± 2.9 (20)	33.4 ± 11.2 (8)
Fence line	*D*	54.0 ± 16.0 (75)	77.2 ± 28.6 (13)
(G, H, J, K)	*S*	21.2 ± 7.2 (37)	—

production of small mammals on the study area (Groves and Keller 1983a). Next, movement data were tested for differences among habitats within a season. Lastly, data were pooled among habitats to test for differences in movement between sexes and between age classes within a season.

Within any season, an animal was recaptured in no more than six trapping periods; the majority of animals were recaptured four times. Only animals that remained on a grid or trapline during their recapture history were included in the movement analysis, except those animals that moved the short distance between grids and adjacent traplines (see Fig. 1). Movements by small mammals from one trapping line or grid to another within the SDA covered distances of more than 200 m, a length well beyond movements previously reported for any species on our study area (Brant 1962, Ramsey 1969). We considered such movements to be outside the normal home range of an animal and classified such individuals as dispersers. Less than 1% of the small mammals marked on an individual grid or trapline dispersed to another grid or trapline within the SDA. These animals, as well as those small mammals that dispersed off the SDA, will be reported on elsewhere.

Skewness and kurtosis values indicated that the movement data were not normally distributed. Additionally, the assumption of homoscedasticity among groups of movement data within each species was violated. Thus, nonparametric procedures, available as SPSS programs (Nie et al. 1975, Hull and Nie 1979), were employed with $\alpha = 0.05$.

RESULTS

A total of 20,689 live-trap nights produced 9,318 captures of 10 species of small mammals during the 15-month study (Groves and Keller 1983a). Sufficient data were obtained to estimate average movements for three species: (1) deer mice (*Peromyscus maniculatus*), montane voles (*Microtus montanus*), and (3) Ord's kangaroo rats (*Dipodomys ordii*). Additionally, limited movement data were obtained for Great Basin pocket mice (*Perognathus parvus*).

Kruskal-Wallis (K-W) analyses of variance or Mann-Whitney U tests were used to analyze differences in movement among habitats by *P. maniculatus* in each season (Table 1.). No significant differences in movement (*D, S,* or *M)* among habitats were detected for *P. maniculatus*[3]. Subsequently, data from different habitats were pooled to produce a single estimate of movement in each season for *D, S,* and *M*.

For *D. ordii* and *M. montanus*, movement data by habitat were only estimated for two seasons because of insufficient sample sizes in other seasons. Mann-Whitney U tests were used to analyze differences in movement between crested wheatgrass and fenceline habitats for both *D. ordii* and *M. montanus* (Table 2). No significant differences in movement between fenceline and crested wheatgrass habitats were detected for *D. ordii* in either summer or autumn by any movement statistic (*D, S,* or *M*). In spring, *M. montanus* moved significantly ($P \leq .05$) greater distances in fenceline habitat than crested wheatgrass habitat as indicated by *D* and *M*. No significant differences in movement between habitats were found for *M. montanus* in summer. Subsequently, data from different habitats were pooled for both *D. ordii* and *M. montanus* to produce a single estimate of movement in each season for *D, S,* and *M*.

A K-W analysis of variance followed by multiple range tests indicated that *P. maniculatus* moved longer distances in spring and summer than other seasons, as estimated by *D* or *M* ($P \leq .05$, Fig. 2a). Seasonal estimates of *D* ranged from approximately 22 m in autumn and winter to 32 m in spring and summer. Estimates of *D* and *M* were significantly different ($P \leq .05$) among spring, summer, and autumn periods for *D. ordii* (Fig. 2b). There was a trend of decreasing range of movement from spring to autumn, with *D* ranging from approximately 72 to 35 m in these periods. Because only a few *D. ordii* were captured in winter (Groves and Keller 1983a), movements could not be estimated for this season. Both *D* and *M* were significantly greater ($P \leq .01$) in winter and summer compared to spring and autumn for *M. montanus* (Fig. 2c). Estimates of *D* ranged from approximately 70 m in winter and summer to 37 m in spring and autumn.

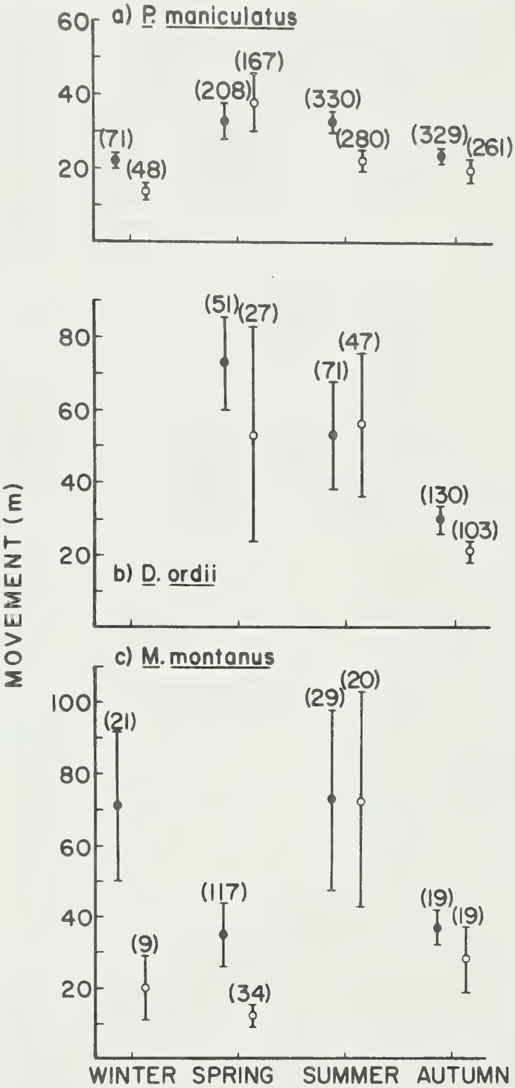

Fig. 2. Seasonal estimates of *D* and *S* for *P. maniculatus* (a), *D. ordii* (b), and *M. montanus* (c) on and adjacent to the Subsurface Disposal Area. Closed circles = *D*; open circles = *S*; bars = S.E.; sample sizes are in parentheses.

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[3] Because estimates, errors, and sample sizes for *M* were similar to *D* for all species, these data were excluded from the text but are available from the authors.

TABLE 3. Estimates of movement (m) (± S. E. (n = number of animals) for male and female *Microtus montanus* and *Dipodomys ordii* on and adjacent to the Subsurface Disposal Area. All pairs of male and female movements shown in the table were significantly different ($P < .05$).

Species	Season	Statistic	Male	Female
M. montanus	Spring	D	36.6 ± 6.0 (40)	26.6 ± 10.2 (56)
	Autumn	S	41.4 ± 16.7 (8)	6.0 ± 2.1 (11)
D. ordii	Spring	D	44.2 ± 6.0 (31)	21.5 ± 4.2 (20)
	Summer	D	37.8 ± 5.0 (36)	43.2 ± 22.4 (35)

Short-term movements (S) were not significantly different among seasons for any species, but they were generally less than D for all species.

A series of Mann-Whitney U tests was used to detect differences in movement (D and S) between males and females within each season. No significant differences in movement were found between male and female *P. maniculatus* in any season. In spring male *M. montanus* and male *D. ordii* moved greater distances than females, as indicated by D (Table 3). In fall male *M. montanus* moved greater distances within trapping sessions (S) than females (41 m vs. 6 m), although sample sizes were small for this comparison. Lastly, female *D. ordii* moved greater distances than males in summer.

Mann-Whitney U tests were also used to detect differences in movement (D and S) between age classes for *P. maniculatus* and *M. montanus*. The mean weight at sexual maturity was used to separate juveniles from adults (Groves 1981). No distinctions were made between juvenile and adult *D. ordii* because of difficulties in assessing external sexual characteristics. No significant differences in movement between age classes of *P. maniculatus* were observed in any season. For *M. montanus*, juveniles moved significantly greater ($P \leq .05$) distances between trapping sessions (D) than adults in spring (55.2 ± 20.2 m ($n = 10$) vs. 15.6 ± 2.5 m ($n = 36$)). Additionally, juvenile *M. montanus* moved greater ($P \leq .05$) distances within a trapping session (S) than adults (53.8 ± 29.6 m ($n = 4$) vs. 14.8 ± 9.9 m ($n = 8$)), although sample sizes were small for comparative purposes.

Although sufficient sample sizes were not available to estimate seasonal movements by *P. parvus*, D and M were estimated by pooling data from spring and summer. The majority of these values were determined from recapture records on Grids A and B in crested wheatgrass stands and Grid M in sagebrush habitat. Average distance between successive captures (D) ± S.E. for *P. parvus* was 45.0 ± 15.8 m ($n = 14$); maximum distance between successive captures (M) was 60.8 ± 26.3 m ($n = 14$).

DISCUSSION

Local movements by small mammals have received considerable attention in the ecological literature. Most studies published to date have concentrated on home ranges (expressed in areal terms) of individual species as determined by live trapping on grids for short periods of time. Because our primary objective was to determine the distance that a small mammal could transport contaminated material, we abandoned the concept of home range in favor of data on the magnitude of average linear movements by small mammals occupying the Subsurface Disposal Area.

On the SDA, *P. maniculatus* showed significantly reduced movements in autumn and winter compared to spring and summer. Colder temperatures and a concomitant reduction in activity may have been responsible for the lesser movements in these seasons. Stebbins (1971) has documented periods of torpor for *P. maniculatus* in Canada during periods of snow and cold. Similarly, *D. ordii* moved significantly lesser distances in autumn compared to spring and summer. This observation, coupled with the fact that we captured few *D. ordii* in winter (Groves and Keller 1983a), suggests that cold weather may also affect activity in this species. O'Farrell (1974) previously reported that *D. ordii* may enter periods of torpor during cold weather.

No significant differences were found between movements of male and female *P. maniculatus* on the SDA, although adults did move greater lengths than juveniles in summer. Both of these results are in agreement with the findings of Brant (1962). Stickel (1968) noted that immature *Peromyscus* remain near the natal site until the dispersal period that coincides with sexual maturity. Consequently juvenile *P. maniculatus* on the SDA could be expected to show reduced linear movements when compared to adults. In spring juvenile *M. montanus* moved significantly greater distances than adults. These longer movements may have resulted from juveniles dispersing from an increasing *M. montanus* population (Groves and Keller 1983a), a phenomenon reported by several authors for microtine populations (Myers and Krebs 1971).

No data on movements have been published for *P. parvus*. Our data indicated that this species moved approximately 45 m between successive captures (*D*) in crested wheatgrass habitat during spring and summer. Thus, *P. parvus* exhibited linear movements slightly less than *D. ordii*, a larger rodent in the same family (Heteromyidae).

In addition to the grids and traplines located on the SDA for assessing rodent populations there, dispersal from the area was estimated with subsampling systems used to enumerate the fraction of the populations that permanently leave the SDA. Although a variety of factors affect the degree of accuracy of such estimates (Keller 1978), our data suggest that only 22% of the small mammals occupying the SDA dispersed on an annual basis. Thus, the majority of movements by small mammals occupying the disposal area were found to occur within its boundaries. An obvious corollary is that the majority of contaminated small mammals also remain within the SDA during their movements.

Data from the radioecology aspects of our study indicated that some *P. maniculatus* and *D. ordii* on the SDA received radiation doses significantly higher than animals from control areas (Arthur et al. 1986). In addition, concentrations of several radionuclides in *P. maniculatus* tissues from the SDA were significantly higher than those from control areas (Arthur et al. in press a). Coyote fecal samples collected adjacent to the SDA boundary contained elevated concentrations of one radionuclide, presumably from uptake of contaminated small mammals (Arthur and Markham 1982). Because average linear movements by small mammals on the SDA range from 20 to 70 m, it is likely that most of the primary redistribution of contaminated material by small mammals via predation occurs within this range from the point of contamination on the SDA. This type of information should be helpful to waste management personnel in implementing a biotic monitoring plan.

The environmental consequences of radiation doses and radionuclide uptake by small mammals on the SDA are likely minimal because the overall amount of radioactivity transported by small mammals off the SDA is small (Arthur et al. in press, 1986) and no adverse impacts to small mammals on the SDA have been observed. Beyond the practical application of these movement data, this study has also provided new information on linear movements by small mammals in crested wheatgrass, Russian thistle, and sagebrush habitats, all common in the Great Basin. Prior to this study, no information was available on movements by *P. parvus*; data on linear movements by *P. maniculatus, D. ordii*, and *M. montanus* were not previously reported for any of the above habitats. Therefore, our movement data contribute new information to the natural history of these four small mammal occupants of the Great Basin.

ACKNOWLEDGMENTS

We thank C. Levesque for field assistance and C. Nimz for extensive aid in computer programming. O. D. Markham and J. E. Anderson critically reviewed the manuscript. This research is a contribution from the INEL Site Ecological Studies Program, supported by the Office of Health and Environmental Research and the Nuclear Fuel Cycle and Waste Management Division, U. S. Department of Energy. B. L. Keller also received support from the Faculty Research Committee (Grant 412), Idaho State University.

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ROLE OF THREE RODENTS IN FOREST NITROGEN FIXATION IN WESTERN OREGON: ANOTHER ASPECT OF MAMMAL–MYCORRHIZAL FUNGUS–TREE MUTUALISM

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ABSTRACT.—To determine the role of the California red-backed vole (*Clethrionomys californicus*), the northern flying squirrel (*Glaucomys sabrinus*), and the deer mouse (*Peromyscus maniculatus*) in the nitrogen cycle of forest stands in western Oregon, bacterial colonies were isolated and purified from feces, and their nitrogen-fixing ability measured by acetylene-reduction assay. The ability of the bacterial species *Azospirillum* sp. to withstand freezing was also tested. Fecal extracts were used to test whether fecal pellets can provide the nutrients necessary for growth of the bacteria. All the feces tested contained viable nitrogen-fixing bacteria, and both species can survive drying and one can survive freezing. *Azospirillum* colonies grew well on liquid medium but required yeast extract for growth and nitrogenase activity. Fecal extracts from flying squirrels and chickarees (*Tamiasciurus douglasi*) were as effective as the yeast. The results suggest another link in the chain of mutualism that unites small mammals, mycorrhizal fungi, and forest trees.

Some small forest-dwelling rodents help maintain productivity of forested ecosystems by disseminating viable spores of hypogeous, mycorrhizal fungi (Kotter and Farentinos 1984, Maser et al. 1978, McIntire 1984, Rothwell and Holt 1978, Trappe and Maser 1976). Nitrogen-fixing bacteria have recently been found in fungal sporocarps eaten by small mammals (Hunt and Maser 1985, Li and Castellano 1985, Maser et al. 1978). To determine whether small mammals play a role in the nitrogen balance of the forest by eating hypogeous fungal sporocarps and thereby dispersing the bacteria, we sought answers to these questions:

- Do feces of forest-dwelling rodents contain nitrogen-fixing bacteria?
- Are these nitrogen-fixing bacteria viable after passage through a rodent's intestinal tract?
- Can these bacteria survive freezing, drying, and high temperature?
- Do the fecal pellets provide the nutrients necessary for growth of nitrogen-fixing bacteria?

We studied three common and widely distributed forest rodents: the deer mouse (*Peromyscus maniculatus*), the California red-backed vole (*Clethrionomys californicus*), and the northern flying squirrel (*Glaucomys sabrinus*).

The deer mouse, ubiquitous throughout most of North America, feeds on fruits, seeds (including conifer seeds), and hypogeous, mycorrhizal fungi (Hunt and Maser 1985, Maser et al. 1978, 1981). The red-backed vole ranges south of the Columbia River, throughout the forested areas of western Oregon into northwestern California, and from the Pacific Coast to the crest of the eastern Cascade Range (Maser et al. 1981). It eats mostly hypogeous fungal sporocarps (Maser et al. 1978, Ure and Maser 1982). The flying squirrel, a nocturnally active inhabitant of most coniferous forests throughout temperate North America, also eats mostly fruiting bodies of hypogeous, mycorrhizal fungi (Maser et al. *Food habits*, 1985; Maser et al. *Northern flying squirrel*, 1985).

We recognize that more quantitative data may be desired than is found in this paper. Our data are the first reported for the following interactions, however, and we are only now determining what quantitative questions can and need to be asked. Further, we have not found a way or person to identify the unknown bacteria and yeasts that we encounter.

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TABLE 1. Acetylene reduction by bacteria isolated from small mammal feces.

Bacterium isolated	Source	Acetylene reduction (nmole ethylene/ mg protein per hr)
Azospirillum sp.	California red-backed vole	167.0[1]
Azospirillum sp.	Northern flying squirrel	88.6[2]
Clostridium butyricum	Deer mouse	344.0[1]

[1] Average of 5 replicates
[2] Average of 3 replicates

METHODS

To determine if nitrogen-fixing bacteria survive passage through rodent digestive tracts, techniques for fecal collection and laboratory techniques were developed to isolate and purify bacterial colonies from rodent feces (Li and Maser, 1986). Acetylene-ethylene assay for nitrogenase activity as an indication of nitrogen-fixing ability was as described by Hardy et al. (1968). Yeast populations in feces were determined by dilution-plating on sodium albumenate agar (Waksman and Fred 1922).

To test the ability of *Azospirillum* sp. to withstand freezing, flying squirrel feces were held at −17 C (1 F) for three months. The feces were thawed and the bacteria isolated, grown, and tested for nitrogenase activity (Li and Maser, in press; additional details on file, Forestry Sciences Laboratory, Corvallis, Oregon 97331).

Azospirillum sp. isolated from feces of the flying squirrel were used to test whether fecal pellets provide the nutrients necessary for growth of nitrogen-fixing bacteria. We used fecal extracts from both the flying squirrel and the chickaree (*Tamiasciurus douglasi*), a diurnal tree squirrel that shares the flying squirrel's habitat in the Pacific Northwest. Fecalextracts were prepared by homogenizing the fecal pellets in deionized water (2:100 w/v) in a Polytron with a saw-tooth generator, 165 x 12 mm, at maximum speed for 1 min. Debris was removed by centrifugation for 30 min at 14,500 x g. The supernatant was filter-sterilized, and 0.2 ml was added to 20 ml of Döbereiner's nitrogen-free liquid medium (Döbereiner and Day 1976).

RESULTS AND DISCUSSION

Feces of all the small mammals we tested contained viable nitrogen-fixing bacteria. *Azospirillum* sp.—a microaerophilic, nitrogen-fixing bacterium (Lakshmi et al. 1977)—was isolated from feces of one red-backed vole and five flying squirrels. *Clostridium butyricum*—an anaerobic, nitrogen-fixing bacterium (Buchanan and Gibbons 1974)—was isolated from feces of seven deer mice. The bacteria not only survived passage through the digestive tracts but also grew and reduced acetylene in vitro (Table 1).

Most bacteria do not survive freezing without desiccation because they rupture on thawing; thus, bacteria to be stored are usually freeze-dried (Gherna 1981). *Azospirillum* sp. can survive freezing in the feces, however, and *C. butyricum* forms an endospore stage that should also be able to survive freezing.

Azospirillum sp. survived at least 15 years in air-dried soil at 28 C ± 2 C (82 ± 4 F) (Lakshmi et al. 1977). In our study *C. butyricum* survived 3 months in air-dried feces, presumably in the endospore form, and it retained the capacity to reduce acetylene.

Many workers have used yeast extract or yeast extract combined with vitamins to promote nitrogenase activity of acetylene-reducing bacteria (Barber and Evans 1976, Haahtela et al. 1981, Murray and Zinder 1984, Rennie 1981, Tyler et al. 1979). The *Azospirillum* colonies grew well on nutrient agar or trypticase soy agar, and they reduced acetylene when grown under conditions of 99% nitrogen and 1% oxygen. The bacterium required yeast extract for growth and nitrogenase activity (Table 2). Controls without acetylene were also assayed with negative results. Extracts from the feces of flying squirrels and chickarees were as effective as yeast extract for inducing nitrogenase activity. Addition of vitamins into the fecal extract proved unnecessary for growth and nitrogenase activity of *Azospirillum* sp. (Table 2).

Yeast extract, a component of many standard culture media (Tuladhar and Rao 1985),

TABLE 2. Influence of additives on acetylene reduction by *Azospirillum* sp. in Döbereiner's nitrogen-free liquid medium (Döbereiner and Day 1976).

Growth condition	Acetylene reduction[1/] (nmoles ethylene/mg protein per hr)
Medium with:	
Yeast extract	71.4
Yeast extract and vitamins	88.6
Vitamins	0
Flying squirrel fecal extract	75.2
Chickaree fecal extract	109.7
Medium without:	
Yeast extract and vitamins	0

[1/] Average of 3 replicates each

is also necessary to the nitrogen-fixing bacteria in vitro (Table 2). We found (in three replications) that fecal pellets of deer mice contained yeast populations that ranged from 33,000 to 40,000 propagules per fecal pellet. A pure culture of yeast and a purified culture of *Azospirillum* sp., both isolated from feces of the flying squirrel, were placed in a nitrogen-free medium and incubated for five days at 30 C (86 F). Results (two replicates each) indicated that the yeast propagules promoted growth and nitrogenase activity of the bacterium. *Azospirillum* sp. alone or yeast propagules alone in Döbereiner's liquid medium exhibited no nitrogenase activity, but *Azospirillum* sp. and yeast propagules together in Döbereiner's liquid medium formed 43 nmoles from acetylene per sample per 17 hr.

Viable nitrogen-fixing bacteria, yeast, and spores of hypogeous, mycorrhizal fungi all survived passage through the digestive tracts of rodents. (Viability of the mycorrhizal fungus spores was tested in studies with seedlings and will be published elsewhere.) The fecal pellets contained the complete nutrients for the nitrogen-fixing bacteria. These findings have several implications for forest habitats. Inoculation of soil with organisms carried in rodent feces is probably common in forest ecosystems. For example, *Azospirillum* sp. can penetrate plant roots (Lakshmi et al. 1977, Patriquin and Döbereiner 1978) and is able to survive for 15 years in stored, air-dried soil (Lakshmi et al. 1977). The fossorial red-backed voles and arboreal flying squirrels are obligate forest-dwellers. When they dig at the bases of trees, the organisms in their feces can inoculate rootlets with nitrogen-fixing bacteria, yeast, and spores of mycorrhizal fungi.

The deer mouse is one of the first small mammals to occupy clearings after logging or fire, so it could inoculate the soil, even soil that has been severely altered by a hot fire. Although the spores of mycorrhizal fungi may not survive high surface temperatures in openings, they could survive under large woody debris on the soil surface where deer mice are active or below the soil surface in rodent burrows. Unlike the fungal spores, the nitrogen-fixing bacterium *C. butyricum* has a built-in survival mechanism (the endospore) by which it can withstand temperatures up to 80 C (176 F) (Simbert and Krieg 1981).

Small rodents have often been seen as detrimental to timber management (Campbell 1982, Crouch and Radwan 1975, Hooven 1975, Sullivan 1979, 1980), and poisons and habitat manipulation have been used against them. But the more forests are altered by human actions, the more evident becomes the need to understand the interactions of all the organisms in the ecosystem. How each component functions is often far more complex than might be anticipated, and the role it plays may be essential in maintaining ecosystem health.

ACKNOWLEDGMENTS

We thank J. W. Witt for helping obtain fresh flying squirrel droppings; D. K. Grayson, R. Molina, R. F. Tarrant, and P. D. Weigl for reviewing the paper; G. Bissell for typing the various drafts. This paper represents a partial contribution (No. 15) of the project entitled "The Fallen Tree—An Extension of the Live Tree." Cooperating on the project are the U.S. Department of the Interior, Bureau of Land Management; U. S. Department of Agriculture, Forest Service, Pacific Northwest Research Station; Oregon State University, Department of Forest Science; U.S. Department of Agriculture, Agricultural Research Service; and Oregon Department of Fish and Wildlife.

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CANIDS FROM THE LATE PLEISTOCENE OF UTAH

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ABSTRACT.—Two canids, *Vulpes vulpes* and *Canis lupus*, are recorded from shoreline deposits of Lake Bonneville in north central Utah. Both species are new records in the Pleistocene sediments of Utah and add to our scarce knowledge of the large carnivores that inhabited the shoreline environments of Lake Bonneville.

The sand and gravel quarries in the shoreline deposits of Lake Bonneville historically have been the most important sources for late Pleistocene vertebrate fossils in Utah. The Lake Bonneville shoreline mammalian fauna has been partially reviewed by Nelson and Madsen (1978, 1980, 1983), Stokes and Condie (1961), and Stock and Stokes (1969). Miller (1976) described the Silver Creek local fauna from the mountains 20 miles east of Salt Lake City, whereas Heaton (1985) documented the late Pleistocene to Recent Crystal Ball Cave local fauna from westernmost Utah. We report the addition of two canids, the fox, *Vulpes vulpes*, and a wolf, *Canis lupus*, to the Bonneville fauna.

STRATIGRAPHY AND LOCATION

The wolf specimens (UVP 100; UVP 101) and one of the fox dentaries (UVP 082) were collected from what was locally known as the Hardman Gravel Quarries (NW 1/4 and NE 1/4, Sec. 32, T1N, R1E, Salt Lake County) in northern Salt Lake City, an area now largely obscured by large homes and the Ensign Elementary School. Both specimens were collected by Golden York, longtime curator of geology in the University of Utah, Department of Geology Museum. The second fox specimen was collected in 1935 near Bacchus, Utah, southwest of Salt Lake City (locality number, 42SL126V in Sec. 8, T25S, R2W), by Mr. A. V. Jenkins. This latter specimen was found in association with several musk ox (*Symbos cavifrons*) vertebrae.

The Hardman Gravel Pit (locality number, 42SLOOIV), at an elevation of 4,800–5,000 ft, yielded sand and gravel from the shoreline deposits near the maximum level of Lake Bonneville. Nelson and Madsen (1980), in following Morrison (1965), thought that the Hardman Quarry was in the Alpine Formation and deposited during the time interval of 33,000–68,000 years BP. However, Scott et al. (1983) have shown that the Alpine is not a valid formational designation. Currey et al. (1983) have placed these quarries at the Bonneville level of the Bonneville Lake Cycle, with deposition occurring around 14,500–18,000 years BP.

All specimens have been curated and entered into the Paleontology Collections of the Antiquities Section, Utah Division of State History (UVP). The specimens from the recent mammal collection of the University of Utah are identified by the initials UM.

SYSTEMATIC PALEONTOLOGY

Class	Mammalia
Order	Carnivora
Family	**Canidae**

Canis lupus Linnaeus, 1758
Gray Wolf

MATERIAL.—UVP 101, right M^1-M^2 with fragments of palatine and maxilla (Fig. 1); UVP 100, left P^4 with alveoli for P^3, M^1 and interior roots of M^2 (Fig. 2). These specimens are most likely from the same individual.

DISCUSSION.—Nowak (1979) recognized four species of wolves from the late Pleistocene of North America: (1) *Canis armbrusteri*, an early? Irvingtonian to early Rancholabrean form; (2) *C. dirus*, the Rancholabrean to early Recent dire wolf; (3) *C.*

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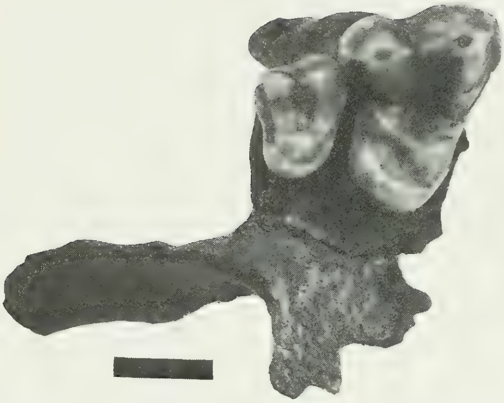

Fig. 1. *Canis lupus*: UVP 101, occlusal view of right M^1–M^2. Solid bar represents 1 cm.

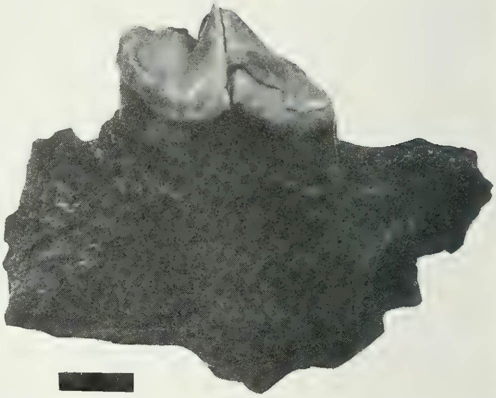

Fig. 2. *Canis lupus*: UVP 100, lateral view of left P^4. Solid bar represents 1 cm.

TABLE 1. Tooth dimensions in samples of *Canis lupus*, *C. dirus*, and the Bonneville specimen. The measurement is the maximum anteroposterior length of the crown of P^4 measured on the outer side. Measurements of *C. lupus* and *C. dirus*, with the exception of the Utah specimen, are from Nowak (1979).

Sample	N	OR	X
C. lupus, male, Recent	233	22.2–30.5	25.92
C. lupus, female, Recent	146	22.2–28.2	24.79
C. lupus, Pleistocene, Maricopa	6	23.3–28.5	26.53
C. lupus, Pleistocene, Rancho La Brea	11	23.0–29.2	26.19
C. dirus, Pleistocene, Maricopa	4	31.0–32.5	31.90
C. lupus, Recent, Utah	1	—	12.31
UVP 100, Pleistocene, Utah	1	—	29.60

rufus, the early Irvingtonian to Recent, but poorly known, red wolf; and (4) the late Irvingtonian to Recent gray wolf, *C. lupus*. The largest collections of late Pleistocene wolves have come from the southern California tar pits—McKitterick, Maricopa, and especially Rancho La Brea, where a minimum of 1,646 dire wolves, but less than 15 gray wolves, have been documented. Most other collections in the United States represent single, or small, samples from cave deposits.

Nowak (1979) believed that *C. lupus* evolved in Asia, whereas *C. dirus* arose in North America. However, *C. lupus* ultimately "prevailed over the dire wolf, either through competition or because of external factors, and established itself as the major large predator of North America." Terminal extinction dates for the dire wolf are around 9500 BP. (Kurten and Anderson 1980), whereas the gray wolf is still extant in North America. However, modern man has extirpated most of these predators from their original range in the contiguous United States, and but a single large population remains in northern Minnesota (Nowak 1979).

Dire wolves were generally larger than gray wolves, having a stockier build and relatively shorter limbs. Most wolves are specifically identified on the basis of their dentition, even though there is some size overlap in these dimensions (Tables 1 and 2). The Bonneville specimen falls into the general size range of a large gray wolf or a small dire wolf.

Both *C. lupus* and *C. dirus* have similar upper fourth premolars that lack a prominent deuterocone and lingual cingulum (Fig. 2). However, the length of P^4 on *C. dirus* is generally much longer than on *C. lupus* (Table 1). Both species have rather undiagnostic, small, second upper molars.

In the first upper molar both species have a large paracone and metacone. However, *C. lupus* generally has a large hypocone with a complete anterolingual cingulum that joins the hypocone. In *C. dirus* the hypocone is

TABLE 2. Tooth dimensions in samples of *Canis lupus*, *C. dirus*, and the Bonneville specimen. The measurement is the maximum transverse diameter of M^2 from the outermost point to the innermost point of the crown. Measurements of *C. lupus* and *C. dirus*, with the exception of the Utah specimen, are from Nowak (1979).

Sample	N	O R	X
C. lupus, male, Recent	233	11.4–16.7	13.82
C. lupus, female, Recent	146	11.2–16.3	13.44
C. lupus, Pleistocene, Maricopa	4	12.2–13.7	12.87
C. lupus, Pleistocene, Rancho La Brea	10	12.5–14.3	13.44
C. dirus, Pleistocene, Maricopa	4	14.4–16.0	15.02
C. dirus, Pleistocene, Rancho La Brea	62	13.1–17.0	15.15
C. lupus, Recent, Utah	1	—	12.31
UVP 100, Pleistocene, Utah	1	—	13.53

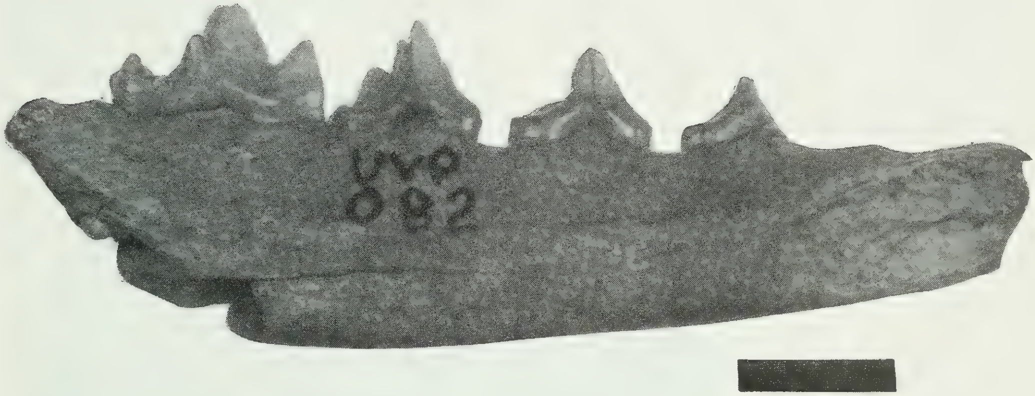

Fig. 3. *Vulpes vulpes*: UVP 82, lateral view of left dentary with P_2–M_1. Solid bar represents 1 cm.

generally reduced, and the incomplete anterolingual cingulum does not reach the hypocone but usually ends somewhere near the protocone. The Bonneville specimen morphologically agrees with the traits assigned *C. lupus* (Fig. 1). The large size may simply be an indication of the Pleistocene age of the specimen because many other late Pleistocene carnivores were larger than their recent descendants (Graham 1981).

Canis cf. *dirus* has been reported from the late Pleistocene Silver Creek fauna in the mountains east of Salt Lake City (Miller 1976). The nearest reported occurrences of *C. lupus* are from the latest Wisconsin to Recent Moonshiner Cave in Brigham County, Idaho (White et al. 1984), and Crystal Ball Cave in Millard County, Utah (Heaton 1985).

Vulpes vulpes (Linnaeus)

Red Fox

MATERIAL.—UVP 82, left dentary with P_2–M_1 and alveoli for P_1 and canine (Figs. 3, 5); UVP 81, left dentary with P_4–M_2 and alveoli for I–P_3 (Fig. 4).

DISCUSSION.—Anderson (1984) recognized five species of late Pleistocene foxes from North America, all of which are extant. The gray fox, *Urocyon cinereoargenteus*, is common in Rancholabrean faunas over much of North America (Kurten and Anderson 1980). The arctic fox, *Alopex lagopus*, is restricted to the arctic regions of North America, Europe, and Asia. It is rarely found in Pleistocene deposits, and in North America has only been reported from the Old Crow River, Yukon Territory (Anderson 1984). *Vulpes velox*, the swift fox, *V. macrotis*, the kit fox, and *V. vulpes*, the red fox are all common in Rancholabrean and Recent faunas of North America. *Vulpes velox* is the dominant small fox in Pleistocene faunas east of the Rocky Mountains, whereas *V. macrotis* is common in the western United States. *Vulpes vulpes* is more cosmopolitan in nature and has been identified in numerous Pleistocene sites from Virginia to California.

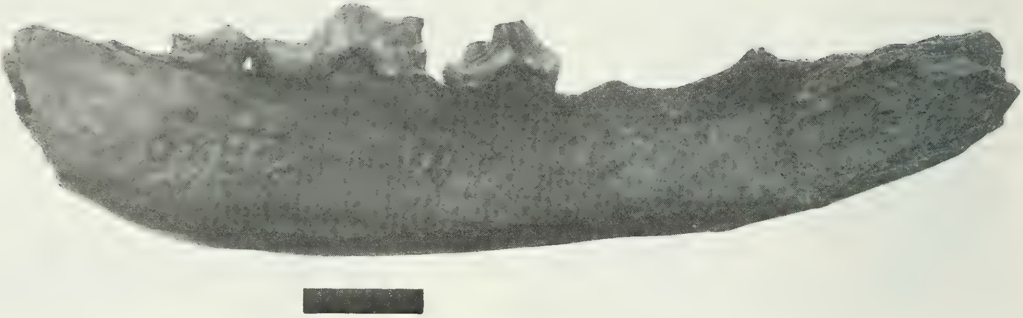

Fig. 4. *Vulpes vulpes*: UVP 81, lateral view of left dentary with $P_4 - M_2$. Solid bar represents 1 cm.

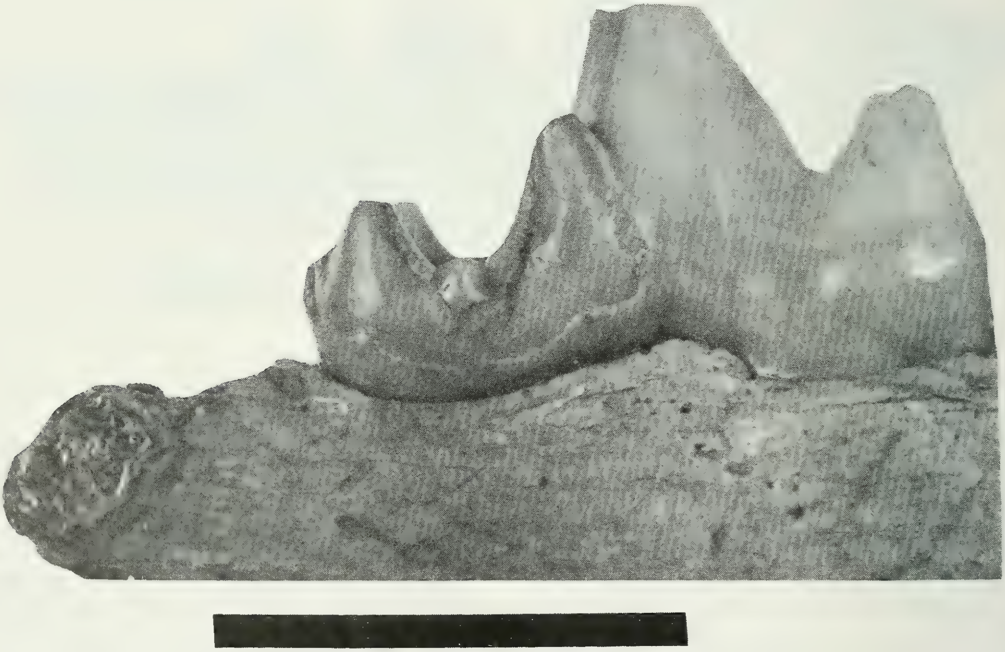

Fig. 5. *Vulpes vulpes*: Lateral view of lower carnassial of UVP 82. Note well-developed cusp at inner junction of talonid and trigonid. Solid bar represents 1 cm.

Members of the genus *Vulpes* differ from *Urocyon* in their relatively smaller molars and the shape of their mandible (Kurten and Anderson 1980). In *Vulpes* the ". . . lower border of the mandible forms an even curve without the lobe seen in *Urocyon*, . . ." whereas in the Arctic Fox ". . . the premolars are higher crowned, M_1 has a distinctly shorter talonid, and the tubercular teeth are more reduced than in *Vulpes*."

The smaller species of *Vulpes*, *V. macrotis* and *V. velox*, may have differences that are only subspecific; recognition in the fossil record is based mainly on the geographic location of the fauna (Anderson 1984, Kurten and Anderson 1980). Both these forms are much smaller (body weight of 1.4–2.9 kg) than *V. vulpes* (4.5–6.7 kg) and are easily recognized in the fossil record.

The Bonneville specimens were compared to the large representation of *V. vulpes* from

TABLE 3. Tooth dimensions in samples of *Vulpes vulpes* from Moonshiner Cave, Idaho, and the shoreline deposits of Lake Bonneville, Utah.

Measurement	N	O R	X	UVP081	UVP082
Length P_2	12	.80–0.90	.85	—	.88
Length P_3	15	.87–1.00	.94	—	.93
Length P_4	14	.82–1.07	.99	1.01	.97
Length M_1	16	1.44–1.63	1.53	10.62	1.40
Length M_2	15	.64–0.73	.70	.70	—
Length P_1–M_2	16	5.27–6.18	5.75	5.68	—

the late Pleistocene to Recent Moonshiner (120 individuals) and Middle Butte (46 individuals) caves in southern Idaho and to Recent specimens (24 individuals) in the University of Utah mammal collections (Table 3). In size and morphology there appears to be little difference in specimens from all localities. UVP 081 lacks the lower third molar and the significance of this feature is unknown (Fig. 4). In Recent specimens from Utah two individuals had a single dentary lacking the M_3; the tooth was present in the other dentaries. In Pleistocene specimens from Little Box Elder Cave, Wyoming, 5 of 19 specimens lack an M_3, whereas all 11 specimens from Jaguar Cave in Idaho have an M_3 (Kurten, written communication, 1985). Approximately 6% of the Moonshiner specimens lack the M_3.

Another variation in the tooth structure can be seen in the lower carnassial (Fig. 3). A small accessory cusp is developed in one of the Bonneville specimens at the internal junction of the trigonid and talonid (Fig. 5). Two Recent specimens from Utah lack this cusp, but it is present in 22 individuals (University of Utah mammal collection); however, the size of this cusp shows considerable variation. Kurten (1967) believed that there might be a connection between the cuspless morphotypes and a cold or continental climate.

Hager (1972) observed 30 Recent specimens of *V. vulpes* from Colorado and Wyoming and reported that all were cusped morphotypes. The significance of the cuspless or cusped morphotypes as an indicator of paleoclimate, therefore, is probably very dubious for *V. vulpes* (Graham 1981).

In examining the Recent specimens of *V. vulpes*, an additional variation in tooth structure was also noted. An adult individual from Kuskokwim Delta, Alaska (UM 18291), lacked a right, lower, first premolar. Therefore, it appears that variation in dental makeup of *V. vulpes* is quite common.

Documented Pleistocene specimens of *V. vulpes* have not been reported from Utah. The species is known from Crystal Ball Cave in western Utah (Heaton 1985), but the exact age of all elements of this fauna is difficult to ascertain, and faunal mixing may have occurred.

ACKNOWLEDGMENTS

We are grateful to Elaine Anderson and Bjorn Kurten for sharing their ideas on Pleistocene canids with us. Norman Negus allowed us access to the University of Utah mammal collections. Fort Hays State University and DINOLAB Inc. provided some financial assistance (Nelson). Jack Jackson from Fort Hays State University provided the photographs.

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NOTE ON FOOD HABITS OF THE SCREECH OWL AND THE BURROWING OWL OF SOUTHEASTERN OREGON

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ABSTRACT.—Diets of the Common Screech Owl (*Otus asio*) and Burrowing Owl (*Athene cunicularia*) from the Great Basin, Malheur County, southeastern Oregon, were studied. Although there was considerable overlap in the diets of these owls, there were differences related to habitat use.

Few data are available on the food habits of owls from the Great Basin of southeastern Oregon. The Barn Owl (*Tyto alba*) is the only one whose food habits have been studied in this part of the state (Maser et al. 1980), although some data are available on food habits of owls from the rangelands of central Oregon: Barn Owl (Maser and Hammer 1972); Great Horned Owl (*Bubo virginianus*) (Brodie and Maser 1967, Maser et al. 1970); Short-eared Owl (*Asio flammeus*) (Maser et al. 1970; Maser et al. *A note on the food habits of the short-eared owl*, 1971); Long-eared Owl (*A. otus*) (Maser et al. 1970), and Burrowing Owl (*Athene cunicularia*) (Maser et al. *Food habits of the burrowing owl*, 1971).

This paper presents information on food habits of the common Screech Owl (*Otus asio*) and the Burrowing Owl in the rangelands of Malheur County, Oregon.

STUDY AREA

The study area, Malheur County, in extreme southeastern Oregon, lies within the Owyhee Upland physiographic province. The major vegetation zone is described as shrub-steppe (characterized by big sagebrush, *Artemisia tridentata*) (Franklin and Dyrness 1973). Plant communities were defined by Dealy et al. (1981), and the more restrictive habitats were described by Bohn et al. (1980) and Maser et al. *Geomorphic and edaphic habitats*, 1979; Maser et al. *Manmade habitats*, 1979).

METHODS

Castings were collected from April 1975 through July 1978. They were placed in plastic bags and were soaked in water before dissection. Prey items were identified to species whenever possible, and individuals were counted. Total counts of leaves and seeds were taken, but other plant parts, fur, and feathers were listed only as the number of pellets in which they occurred. Comparisons between vertebrate and invertebrate foods were based on total percentages. Diversity of prey was calculated for all food items as the number of items per total number of castings.

RESULTS AND DISCUSSION

Vertebrates formed 20.2% of the prey individuals in screech owl diets (Table 1); invertebrates, 79.8% (Table 2). Vertebrates comprised 14.3% of the prey items in burrowing owl diets (Table 3) and invertebrates 85.7% (Table 4).

Vertebrate Prey

Both owls fed heavily on the Ord kangaroo rat (*Dipodomys ordi*), but the kangaroo rat was more important to the Burrowing Owl than to the Screech Owl.

The northern pocket gopher (*Thomomys talpoides*) was important in the diet of the Burrowing Owl but accounted for less than 1% of the Screech Owl diet. The similarity in weight between the Ord kangaroo rat (the average weight of 32 individuals from both

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TABLE 1. Vertebrate foods of the Screech Owl (*Otus asio*) from southeastern Oregon, based on analysis of 205 castings.

Prey item		Number of individuals	Percentage of diet	Number of castings	Percent frequency
MAMMALIA					
Rodentia					
Cricetidae	*Peromyscus* sp.	16	5.2	10	4.9
	Cricetinae unidentified	69	22.6	41	20.0
	Microtinae unidentified	25	8.2	18	8.8
	Microtus sp.	2	0.6	1	0.5
	Lagurus curtatus	11	3.6	10	4.9
Geomyidae	*Thomomys talpoides*	2	0.6	2	1.0
Heteromyidae	*Dipodomys ordi*	39	12.8	32	15.6
	Perognathus parvus	1	0.3	1	0.5
Scuiridae	*Spermophilus* sp.	8	2.6	1	0.5
	Sciuridae unidentified	16	5.2	16	7.8
Lagomorpha					
Leporidae	*Lepus californicus*	1	0.3	1	0.5
	Leporidae unidentified	16	5.2	11	5.4
Mammal	Unidentified	47	15.4	46	22.4
REPTILIA					
Squamata					
Iguanidae	*Phrynosoma platyrhinos*	11	3.6	9	4.4
	Cnemidophorus tigris	1	0.3	1	0.5
Lacertilia	Unidentified	23	7.5	10	4.9
Reptile	Unidentified	11	3.6	11	5.4
AVES					
Columbiformes					
Columbidae	*Zenaida macroura*	1	0.3	1	0.5
Passeriformes	Unidentified	2	0.6	2	1.0
Bird	Unidentified	3	1.0	1	0.5
*Eggshell	Unidentified	—	—	6	
*Feathers	Unidentified	—	—	5	
*Claws	Unidentified	—	—	8	
		305	99.5		

*Not included in total count

central and southeastern Oregon was 56.8 g; Maser, unpublished data), and the northern pocket gopher in Malheur County (61.3 g) probably allowed the Burrowing Owl to exploit both species. These gophers formed only 0.02% of the Burrowing Owl diet in central Oregon (Maser et al. *Food habits of the burrowing owl*, 1971). Northern pocket gophers of the poorly drained lacustrine soils that occur in Malheur County are small (average weight of 25 individuals was 61.3 g) compared with the same subspecies (*quadratus*) from the better drained soils of the Steens Mountain, Harney County (average weight of eight individuals, 94.6 g), and from the sandy soils of central Oregon, Jefferson and Klamath counties (average weight of 47 individuals 67.4 g; Maser, unpublished data). Possibly, the weight difference (6.1 g) between the gophers of central and southeastern Oregon allowed the Burrowing Owl to exploit this prey in one area but not in the other.

Within the family Cricetidae, the Screech Owl had the following taxa available as prey: western harvest mouse (*Reithrodontomys megalotis*), deer mouse (*Peromyscus maniculatus*), canyon mouse (*P. crinitus*), northern grasshopper mouse (*Onychomys leucogaster*), desert woodrat (*Neotoma lepida*), bushy-tailed woodrat (*N. cinerea*), montane vole (*Microtus montanus*), long-tailed vole (*M. longicaudus*), and sage vole (*Lagurus curtatus*). Montane voles were by far more abundant than long-tailed voles (Maser, unpublished data). The family Cricetidae accounted for 40.2% of the vertebrate prey items. The

TABLE 2. Invertebrate foods and vegetation of the Screech Owl (*Otus asio*) from southeastern Oregon, based on analysis of 205 castings.

Prey items		Number of individuals	Percentage of diet	Number of castings	Percent frequency
INSECTA					
Coleoptera					
Carabidae	*Calosoma* sp.	90	7.5	34	16.6
	Near *Anisodactylus* sp.	6	0.5	5	2.4
	Unidentified	3	0.2	3	1.5
	Anisodactylus sp.	7	0.6	1	0.5
Curculionidae	Unidentified	6	0.5	10	4.8
Alleculidae	Unidentified	1	0.1	1	0.5
Tenebrionidae	Unidentified	61	5.1	33	16.1
Scarabaeidae					
	Cyclociphala sp.	41	3.4	30	14.6
	Rutela sp.	1	0.1	1	0.5
	Unidentified	4	0.3	4	2.0
	Paracotalpa granicollis	6	0.5	4	2.0
Silphidae	*Necrophorus* sp.	11	0.9	7	3.4
Coleoptera	Unidentified	21	1.7	20	9.8
Diptera	Unidentified	3	0.2	3	1.5
Hemiptera	Unidentified	1	0.1	1	0.5
Homoptera					
Cicadidae	Unidentified	81	6.7	21	10.2
Hymenoptera					
Formicidae	Unidentified	20	16.6	12	5.9
Lepidoptera	Larvae	3	0.2	1	0.5
Neuroptera	Unidentified	1	0.1	1	0.5
Orthoptera					
Acrididae	Unidentified (mandibles)	424	35.2	48	23.4
Gryllidae	*Gryllus veletis*	59	4.9	35	17.1
	Unidentified (mandibles)	27	2.2	8	3.9
Stenopalmatidae	*Stenopelmatus* sp. (mandibles)	117	9.7	19	9.3
Siphonaptera	Unidentified	2	0.2	1	0.5
ARACHNIDA					
Araneida	Unidentified	4	0.3	4	2.0
Scorpionida					
Vejovidae	*Vejovis boreus*	24	2.0	16	7.8
VEGETATION					
Leaves	*Erigonum*	—	—	41	
*Vegetation		—	—	11	
*Seeds	Unidentified	2	—	1	0.5
*Grass seeds		48	—	3	1.5
		1,204	99.7		

*Not included in total count

subfamily Cricetinae accounted for 27.8% and Microtinae 12.4% of the vertebrate diet.

The Burrowing Owl had the same taxa available as prey within the family Cricetidae as did the Screech Owl, except for the canyon mouse and occasionally the desert woodrat. Cricetidae formed 29.9% of the Burrowing Owl vertebrate diet. The subfamily Cricetinae composed 10.3% and the Microtinae 15.7%. As with the Screech Owl, the montane vole was far more abundant in habitat of the Burrowing Owl than was the long-tailed vole (Maser, unpublished data).

Invertebrate Prey

Although the Screech Owl ate 26 kinds of invertebrates (Table 2) and the Burrowing Owl ate 24 kinds (Table 4), there are some major differences. Beetles accounted for 21.4% of the items in the Screech Owl diet, including Scarabaeidae (4.3%) and Carabidae (8.8%). Beetles were slightly more important to the Burrowing Owl (38.6% of the diet). Although the Burrowing Owl used Carabidae about the same as the Screech Owl (7.8%), Scarabaeidae were more important to the Burrowing Owl (21.7%).

TABLE 3. Vertebrate foods of the Burrowing Owl (*Athene cunicularia*) from southeastern Oregon, based on analysis of 150 castings.

Prey item		Number of individuals	Percentage of diet	Number of castings	Percent frequency
MAMMALIA					
Rodentia					
Cricetidae	*Peromyscus maniculatus*	11	5.4	10	6.7
	Reithrodontomys meglotis	7	3.4	7	4.7
	Microtus sp.	10	4.9	8	5.3
	Lagurus curtatus	13	6.4	11	7.3
Cricetinae	Unidentified	3	1.5	3	2.0
Microtinae	Unidentified	9	4.4	8	5.3
Cricetidae	Unidentified	8	3.9	6	4.0
Geomyidae	*Thomomys talpoides*	21	10.3	21	14.0
Heteromyidae	*Dipodomys ordi*	49	24.1	47	31.3
	Perognathus parvus	11	5.4	11	7.3
	Unidentified	1	0.5	1	0.7
Sciuridae	Unidentified	14	6.9	14	9.3
Mammal	Unidentified	19	9.4	18	12.0
AMPHIBIA	Unidentified	21	10.3	14	9.3
REPTILIA					
Squamata					
Iguanidae	*Phrynosoma platyrhinos*	1	0.5	1	0.7
Reptile	Unidentified	4	2.0	4	2.7
AVES					
Columbiformes					
Columbidae	*Zenaida macroura*	1	0.5	1	0.7
*Feathers				4	
		203	99.8		

*Not included in total count

The other insect order of major importance to both owls was Orthoptera. This item was more important to the Screech Owl (52.0%) than to the Burrowing Owl (34.3%). Within Orthoptera, grasshoppers (Acrididae) were more important to the Screech Owl (35.2%) than to the Burrowing Owl (21.6%), but the Jerusalem cricket (*Stenopelmatus* sp.) was eaten more by the Burrowing Owl (12.7%) than by the Screech Owl (9.7%). The Screech Owl also consumed the cricket (*Gryllus veletis*) (4.9%), but the Burrowing Owl did not.

Prey Diversity

Total prey diversity per casting for the Screech Owl was 0.3 species and averaged 7.4 individual items. The Burrowing Owl was surprisingly close, 0.3 species per casting and averaged 9.5 individuals.

Owls

The Screech Owl generally inhabited riparian zones, abandoned homesteads, and some cliffs (Bohn et al. 1980; Dealy et al. 1981; Maser et al. *Geomorphic and edaphic habitats*, 1979; Maser et al. *Manmade habitats*, 1979; Maser, unpublished data). The Burrowing Owl, on the other hand, was associated with badger (*Taxidea taxus*) burrows, primarily in the basin big sagebrush/bunchgrass and black greasewood (*Sarcobatus vermiculatus*)/grass communities (Dealy et al. 1981; Maser, unpublished data).

Flexibility in selection of habitat by the Screech Owl brought it into contact with a wider prey base than was available to the Burrowing Owl with its more rigid selection of habitat. For example, Screech Owls in cliffs had canyon mice and both species of woodrats available; Screech Owls in abandoned homesteads also had both species of woodrats available and were known to take the desert woodrat (Maser, unpublished data). The Burrowing Owl, however, occupied habitat that was inhospitable to canyon mice and to bushy-tailed woodrats, and the desert woodrat only occasionally inhabited the black greasewood/grass community (Maser, unpublished data).

Both species of owl are opportunistic and catholic in diet (Gleason and Craig 1979; Maser et al. *Food habits of the burrowing*

TABLE 4. Invertebrate foods and vegetation of the Burrowing Owl (*Athene cunicularia*) from southeastern Oregon, based on analysis of 150 castings.

Prey item		Number of individuals	Percentage of diet	Number of castings	Percent frequency
INSECTA					
Coleoptera					
Carabidae	*Calosoma* sp.	51	4.2	36	24.0
	Anisodactylus sp.	31	2.5	13	8.7
	Unidentified	14	1.1	8	5.3
Curculionidae	Unidentified	19	1.6	11	7.3
Scarabaeidae	*Paracotalpa granicollis*	121	9.9	25	16.7
	Cyclocephala sp.	1	0.7	1	0.7
	Rutela sp.	88	7.2	26	17.3
	Unidentified	48	3.9	17	11.3
Tenebrionidae	Unidentified	30	2.5	22	14.7
Silphidae	*Necrophorus* sp.	49	4.0	30	20.0
Elateridae	Unidentified	11	0.9	2	1.3
Coleoptera	Unidentified	1	0.1	1	0.7
Diptera	Unidentified	28	2.3	4	2.7
Homoptera					
Cicadidae	Unidentified	13	1.1	12	8.0
Hymenoptera					
Formicidae	Unidentified	10	0.1	3	2.0
Braconidae	Unidentified	98	8.0	8	5.3
Lepidoptera	Unidentified (larvae)	7	0.6	3	2.0
Orthoptera					
Acrididae	Unidentified	263	21.6	55	36.7
Stenopelmatidae	*Stenopelmatus* sp. (mandibles)	155	12.7	9	6.0
Insect	Unidentified	2	0.2	2	1.3
	Unidentified (mandibles)	48	3.9	5	3.3
ARACHNIDA					
Scorpionida					
Vejovidae	*Vejovis boreus*	126	10.3	56	37.3
Araneida	Unidentified	3	0.25	3	2.0
Acari	Unidentified	2	0.2	2	1.3
VEGETATION					
*Leaves	*Eriogonum* sp.	103		18	
*Vegetation		17		6	
*Seeds	Grass	52		2	
Feathers	Unidentified	1		1	
		1,219	100.3		

*Not included in total count

owl, 1971; Smith and Wilson 1971; Zarn 1974), and their diets in southeastern Oregon overlapped considerably. They used totally different habitats, however, which physically isolated the owls and avoided competition.

ACKNOWLEDGMENTS

Sam Shaver (Vale, Oregon) helped collect the castings. D. Grayson (Department of Anthropology, University of Washington, Seattle), Z. Maser (Department of Forest Science, Oregon State University, Corvallis), and D. Toweill (Department of Fisheries and Wildlife, Oregon State University, Corvallis) read and improved the manuscript. V. Bissell (USDI Bureau of Land Management, Forestry Sciences Laboratory, Corvallis, Oregon) typed the various drafts. We thank them for their help.

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DISEASES ASSOCIATED WITH *JUNIPERUS OSTEOSPERMA* AND A MODEL FOR PREDICTING THEIR OCCURRENCE WITH ENVIRONMENTAL SITE FACTORS

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ABSTRACT.—On 17 Utah juniper (*Juniperus osteosperma* [Torrey] L.) sites studied in Utah, *Gymnosporangium inconspicuum* was the most common rust fungus, followed in frequency and severity by *G. nelsoni*, *G. kernianum*, and *G. speciosum*. The incidence of *G. kernianum* was correlated with moderate temperatures and greater than average precipitation. True mistletoe, *Phoradendron juniperinum* Engelm., was present on seven sites. Incidence of foliage diseases of the mold-mildew type was low on sites with low spring and summer temperatures and high on sites with high summer and fall precipitation. Wood rot was common, and incidence seemed to be correlated with low winter temperatures and low soil nitrate but not with annual precipitation. Needle blight, shoot dieback, and needle cast symptoms were common and considered of abiotic origin. Their nonparasitic nature was indicated by lack of association with pathogenic organisms and the positive correlation of their incidence with winter injury and summer drought factors. Needle blight was also positively correlated with high soil salinity but negatively with high soil calcium regardless of salinity.

A nonparametric model was developed that accurately predicted the frequency of the mold-mildew type diseases of *J. osteosperma* based on measured environmental site factors.

The pinyon-juniper woodland is a widespread vegetation type in the southwestern United States, estimated to cover from 30 to 40 million hectares (Allred 1964). Historically, pinyon-juniper woodland vegetation has provided numerous benefits including fuel, building materials, charcoal, nuts, Christmas trees, medicines, etc. (Tueller et al. 1979, Hurst 1977, Lanner 1975, Cronquist et al. 1972, Gallegos 1977). About 80% of the total acreage is grazed, contributing significantly to the available forage for livestock and wildlife (Clary 1975), and pinyon-juniper woodlands are becoming increasingly valued for their watershed, aesthetic, and recreational values (Gifford and Busby 1975).

This ecosystem is a large component of the vegetation of Utah (62,705 km^2 or 28.6%, Kuchler 1964), and it has the potential to add substantially to the economic and aesthetic activity of the state. Despite this potential, little research has been done to explore the physiological relationships and autecology of this vegetation type.

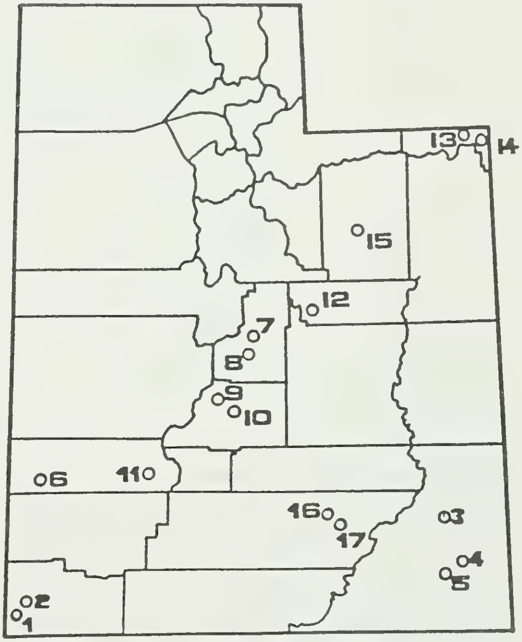

Fig. 1. Location of 17 study sites in Utah.

Many complex environmental factors contribute to the variety of interactions in a pinyon-juniper ecosystem. Consumable "supply factors" of the environment such as light, water, nutrients, oxygen, and carbon dioxide interact with "site quality" or "condition" factors such as temperature and precipitation (Harper 1977). The effects of species density,

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TABLE 1. Description of symptoms and assessment methods for diseases of *Juniper osteosperma*.

Injury	Diseases of *J. osteosperma* symptom or sign	Rating scale
Needle blight	Senescent or decadent foliage or twigs. Terminals may show yellow or red-brown coloration. May or may not show evidence of fungal fruiting bodies.	Percent of the total plant affected
Needle cast	Bare twig terminals from which foliage scale leaves have fallen (twig terminals of living branches).	Percent of the total plant affected
Tip dieback	Senescent or decadent foliage or twig terminals showing brown to grey coloration. May or may not show evidence of fungal fruiting bodies.	Percent of the total plant affected
Pathogen		
Gymnosporangium rusts:		
G. inconspicuum	Presence of follicolous or caulicolous telia having cartiform pedicels accompanied by little or no fasciation of branches.	Rated as light, moderate, or heavy: a) light: 1–3 telial infections in a 2 ft breast high circumference section of tree. b) moderate: 4–10 telial infections in equivalent area. c) heavy: more than 10 telial infections in equivalent area.
G. nelsoni	Presence of galls with irregularly compressed, wedge-shaped telia; on twigs or branches.	Actual or estimated number of galls per tree.
G. kernianum	Presence of well-defined or modified witch's brooms (branch fasciation) with foliicolous, bluntly conical telia.	Actual or estimated number of witch's brooms per tree.
G. speciosum	Presence of cristiform or crenate telia on fusiform swellings.	Actual or estimated number of fusiform swellings per tree.
Wood rot fungi (i.e., *Fomes juniperinum*)	Presence of heart rot or decayed areas in trunk or branches. Fungal fruiting bodies may or may not be present.	Presence rated as light, moderate, or heavy.
Mold and/or mildew (unidentified spp.)	Fungal mycelial growth on foliage.	Presence rated as light, moderate, or heavy.
Mistletoe (*Phoradendron juniperinum*)	Presence of viable mistletoe foliage in tree.	Actual or estimated number of growth areas per tree.

habitable niches, pathogens, seasonality, and roles of predators such as grazing animals influence the diversity and stability of pinyon-juniper woodlands, as do naturally occurring catastrophic events (i.e., fire) or deliberate manipulation or intervention by man.

The ecological dynamics of the pinyon-juniper ecosystem have been studied by Pearson (1920), Woodbury (1947), Daniel et al. (1966), and Vasek (1966) and typically have been oriented toward range and resource management. Synecological studies of pinyon-juniper have included work in latitudinal and elevational patterns (Daubenmire 1943), interactions with understory vegetation (West et al. 1975), paleoecological influences (Cottam 1959), and climatic and edaphic relationships (Beeson 1974, Hunt 1974). Several studies have treated disease and/or insect factors of pinyon pines (McCambridge and Pierce 1974, McGregor and Sandrin 1968, Hepting 1921), but little research in these particular areas has dealt with juniper.

The objectives of this study were to survey the diseases of Utah juniper (*Juniperus osteosperma* [Torrey] L.), particularly those induced by fungi, and to relate their occurrence, frequency, and severity to selected environmental factors in several pinyon-juniper habitats throughout Utah.

MATERIALS AND METHODS

Seventeen representative pinyon-juniper sites in Utah were studied from April to Octo-

TABLE 2. Location of 17 primary juniper study sites in Utah.

Site name	Site no.	Weather station
Jackson Springs	1	St. George
Tobin Bench	2	Veyo Power House
Peters Point	3	Monticello
Alkali Ridge	4	Blanding
Cyclone Flat	5	Natural Bridges Natl. Mon.
Indian Peak	6	Desert Expt. Range
Ephraim	7	Ephraim Sorensens Fld.
Manti	8	Manti
Black Mountain	9	Salina
Triangle Mountain	10	Salina
Beaver Ridge	11	Beaver
Gordon Creek	12	Hiawatha
Dutch John	13	Flaming Gorge
Taylor Flat	14	Allen's Ranch
Rabbit Gulch	15	Hannah
Henry Mountains (Stevens Narrows)	16	Capitol Reef Natl. Park
Henry Mountains (Airplane Flat)	17	Boulder

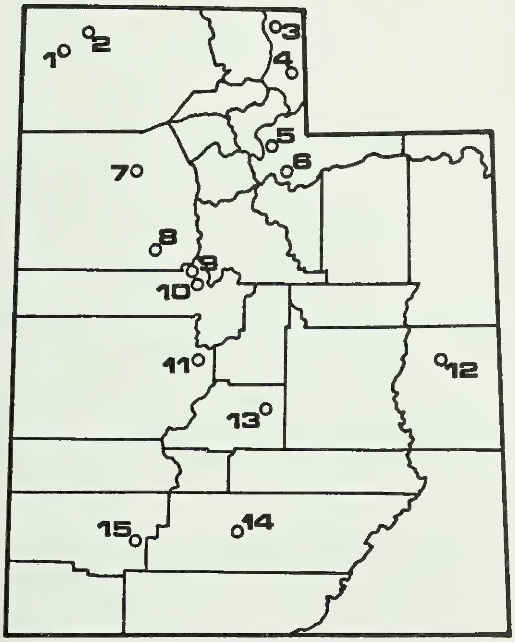

Fig. 2. Observations of four *Gymnosporangium* species in selected Utah sites.

ber 1982 (Fig. 1). Sites were selected for climax pinyon-juniper vegetation and minimal structural disturbance by people, although most sites had a long history of grazing by domestic animals and wildlife. Soils were primarily derived from marine shales, conglomerates, siltstones, and sandstones (Bunderson et al. 1985).

Transects at each site consisted of 96 Utah juniper trees randomly selected by the quarter method (Phillips 1959). Each tree was measured for height, stem diameter, and age and then assessed for signs and symptoms of disease. Diseases were classed in three causal categories: (a) rust fungi (*Gymnosporangium* spp.), (b) miscellaneous fungus diseases (e.g., tip burn, die back, stem decay), and (c) parasitic higher plants. Nonparasitic injury was also assessed. Descriptions of diseases, pathogenic agents, and assessment methods are found in Table 1. The percentage of decadence for each tree was estimated and an overall vigor score (1 = good, 2 = moderate, 3 = poor) was assigned to each tree.

Since some areas of the state were not represented in our 17 primary sites (Table 3), we added 15 additional sites (Fig. 2) in which just the incidence of *Gymnosporangium* rusts was studied. We used the standard U.S. Forest Service ratings as listed in the addendum to Table 4.

Since each site had its own pattern of infection, we calculated severity indexes to reflect both the total number of trees infected with each causal agent and the severity of that infection on each tree (Table 2).

We measured concentrations of several soil mineral nutrients (N, P, K, Ca, Mg, Na, Fe, SO_4) and other soil properties (pH, EC, sand, silt, clay) by digging five soil pits along each transect and pooling samples from the top 12 inches of soil from each pit. Soils were acid digested and analyzed for mineral content using a Technicon II Auto Analyzer and atomic absorption spectroscopy. Temperature and

TABLE 3. Observations of three *Gymnosporangium* species in selected Utah sites.

	G. inconspicuum	*G. nelsoni*	*G. kernianum*
1. Immigrant Pass	C	O	C
2. Rosette	A (*very* heavy)	A	A
3. Bear Lake	C	O	A
4. Hwy 39, 6 mi west of Woodruff	C	A	A
5. Chalk Creek	A (on both foliage and twigs)	C	C
6. Hwy 150—Yellow Pine Campground	O	O	R
7. Hastings Canyon	C	R	C
8. Lookout Pass	O	O (no live galls)	O
9. 12 mi Northeast of Eureka	O	C	C (heavy when present)
10. Silver City	R	O	N
11. Scipio Pass	C	C	A
12. Sego	A (some fasciation)	A (*very* heavy)	N
13. 2 mi south of Fremont Junction	A	O (most galls dead)	O (heavy when present)
14. Escalante Canyon	C	C	N
15. 8 mi east of Parowan	O	C	N

A = Abundant
C = Common
O = Occasional
R = Rare
N = None observed in area

precipitation records were obtained from National Oceanic and Atmospheric Administration recording stations at or near the research sites. For complete descriptions of the 17 primary site locations and weather recording stations, see Table 3. These values were divided seasonally into four quarters: December–February, March–May, June–August, September–November. Location and frequency of alternate hosts for *Gymnosporangium* rusts were also noted.

We used linear correlation coefficients to relate frequencies and severity of the diseases of Utah juniper to the soil factors, temperature, and precipitation. A nonparametric weighted least squares analysis for categorical data tested hypotheses relating interactions between the environmental data and pathogenic factors (Forthofer and Lehnen 1981). The hypotheses were checked for statistical significance and offered as a possible tool to predict the incidence of disease that would occur within a given site if the conditions of the hypotheses were met.

RESULTS AND DISCUSSION

Gymnosporangium Rusts

Frequent occurrences of *Gymnosporangium* spp. on Utah juniper have been recorded in Utah (Arthur 1934, Hodges 1962, Peterson 1967), but these occurrences have not been quantified. Figures 3 and 4 quantify the frequency of the three *Gymnosporangium* rusts we encountered most often on Utah juniper in the 17 transects.

Gymnosporangium inconspicuum Kern was present on a substantial proportion of the trees at 15 of the 17 sites. The caulicolous and/or foliicolous telia of *G. inconspicuum* are inconspicuous and difficult to locate, and probably more trees were infected than recorded. The high frequencies support observations by others that *G. inconspicuum* has a high endemic population in juniper stands throughout Utah (Peterson 1967). We examined the two sites where *G. inconspicuum* was not recorded on three separate occasions without finding any indication of this fungus. Since these sites are located in the St. George area in the warm Mohave Desert ecotype rather than in the cooler Great Basin ecotype, environmental factors may influence the occurrence of this rust in ways other than those we have measured.

We found *Gymnosporangium nelsoni* Arth. in all research sites. The galls stimulated by this rust on stems and branches of *J. osteosperma* varied from 2 to 12 cm in diameter, and both live and dead galls were counted until gall numbers exceeded 300 per tree. Excluding the St. George sites, incidence of

TABLE 4. Description of rating system for diseases of *Juniper osteosperma*.

Infection level = Number of trees infected with pathogen.

Severity

a. *G. inconspicuum* = Average rating of infections per tree
0 = No infection
1 = Light infection
2 = Medium infection
3 = Heavy infection

b. *G. nelsoni* = Average number of galls/tree

c. *G. kernianum* = Average number of witch's broom/tree

Severity Index

a. *G. inconspicuum* = $\dfrac{\text{Proportion of infected trees (expressed as a \%)}}{\text{Site rating} \div 3} \times 100$

b. *G. nelsoni* = $\dfrac{\text{Severity}}{\text{Average number galls/meter} \div \text{proportions of infected trees (\%)}}$

c. *G. kernianum* = $\dfrac{\text{Severity}}{\text{Average height of trees at site} \div \text{proportions of infected trees (\%)}}$

Mold mildew
Severity = Percentage of trees infected;
Severity index = Proportion (%) × percentage infected (severity)

Wood-rotting fungi
Severity = Sum of percentage of trees infected with trunk, branch, twig rot;
Severity index = Proportion (%) × severity

Mistletoe
Severity = Average number of broom/tree; severity index = Proportion (%) × severity

Needle blight
Severity = Average percentage of infection/infected tree; Severity index = Proportion (%) × severity

Needle cast
Severity = Average percentage of mildew on all infected trees (cumulative);
Severity index = Proportion (%) × severity

Tip dieback
Severity = Average percentage of infection/infected tree;
Severity index = Proportion (%) × severity

G. nelsoni was much more variable than that of *G. inconspicuum*.

We found *Gymnosporangium kernianum* Bethel on fewer sites than either *G. inconspicuum* or *G. nelsoni*. This species stimulates shoot fasciations (witch's brooms) on which foliicolous telia are formed. Numbers of brooms per infected tree ranged from 0 to 23 and size of brooms from 3 to 130 cm in diameter. The incidence of *G. kernianum* was considerably less than that of either *G. inconspicuum* or *G. nelsoni*. As with *G. inconspicuum*, only active infections were recorded.

Correlations between temperature and precipitation in our research sites indicate that *G. kernianum* is favored by moderate temperatures and a greater than average annual precipitation, particularly during the summer (Tables 5, 6).

We found a fourth species, *Gymnosporangium speciosum*, on only one primary site (Site 12) and one supplementary site (Sego). It forms bright orange cristiform or crenate telia on fusiform stem swellings, with loose fascications usually associated with the infected area.

Variation in host susceptibility complicates establishing cause and effect relationships with physical environmental factors for *Gymnosporangium* rusts. Differences in resistance to cedar-apple rust have been known for many years (Moore 1940) as well as differences in pathogenicity of the rust (Aldwinkle 1975). It has been suggested that the genetic variability

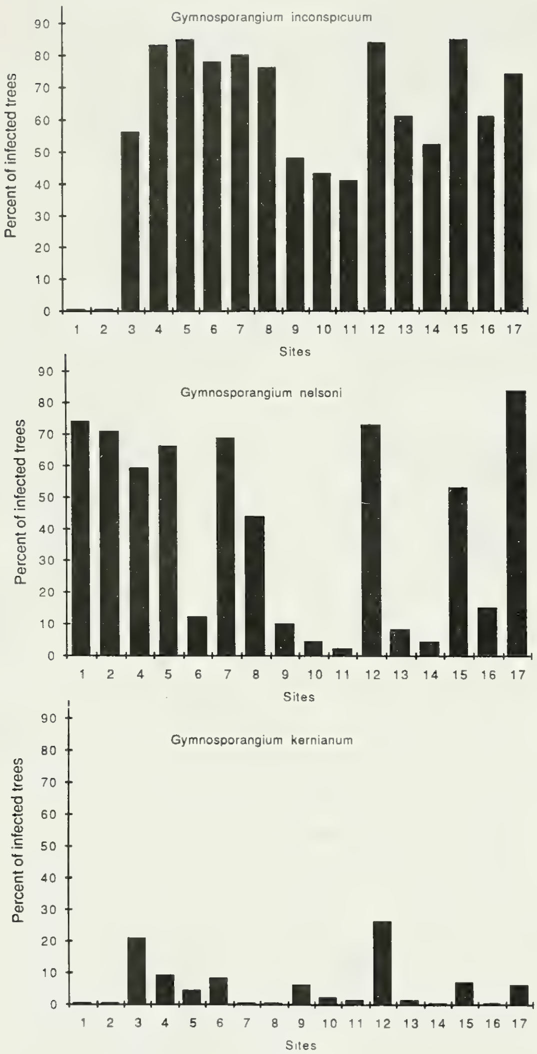

Fig. 3. The percent of infected trees (*Juniperus osteosperma*) in relation to three rusts. Top chart (*Gymnosporangium inconspicuum*), middle (*Gymnosporangium nelsoni*), bottom (*Gymnosporangium kernianum*).

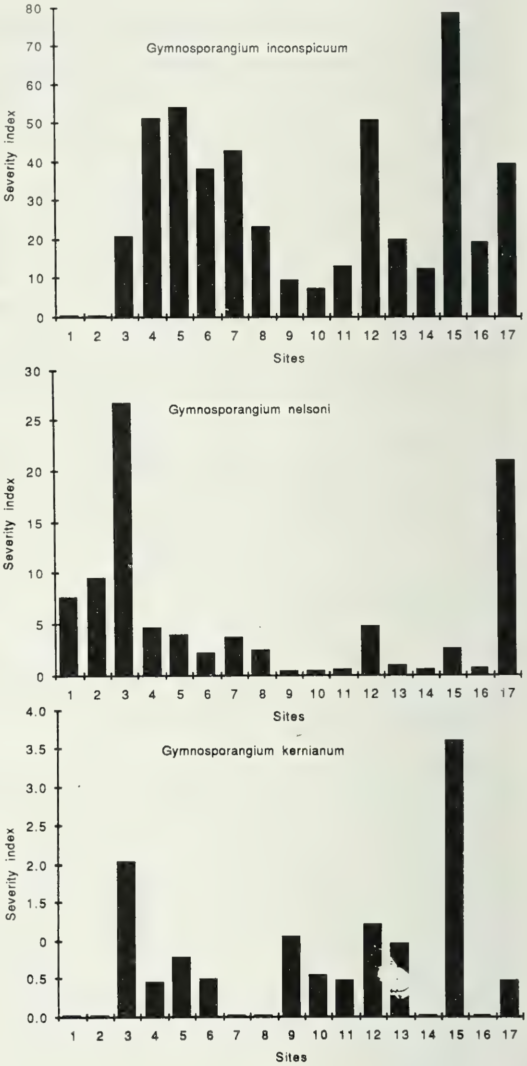

Fig. 4. The severity index of three rusts (top) *Gymnosporangium inconspicuum*, (middle) *Gymnosporangium nelsoni*, (bottom) *Gymnosporangium kernianum* on *Juniperus osteosperma* trees.

of Utah juniper may surface in the average number of stems in any given stand (Kimball Harper, personal communication). After pooling the data from the 17 sites, we found a correlation between environmental parameters such as amount of precipitation and number of juniper stems ($\alpha = 0.01$ with average annual precipitation, $\alpha = 0.05$ with summer precipitation), indicating that as the total precipitation decreases the number of stems increases. However, there are also positive correlations between increasing numbers of stems and the increased frequencies of the various rusts ($\alpha = 0.05$ for *G. nelsoni*, $\alpha = 0.10$ for *G. kernianum*). *Gymnosporangium inconspicuum* has been described as either foliicolous or caulicolous, and our data indicate that *G. inconspicuum* on the foliage correlates positively to the number of stems of *J. osteosperma* ($\alpha = 0.10$) and the caulicolous form of *G. inconspicuum* correlates negatively to the number of stems ($\alpha = 0.10$). Further studies are needed to understand these correlations.

Miscellaneous Fungus Diseases

Several types of wood-decay fungi were indicated along our transects (Figs. 6, 7) by

TABLE 5. Correlations between *J. osteosperma* diseases and insects and temperature in the different time quarters (Q).

	5-year average				Hi Q	Low Q	Annual	5-year	5-year
Pathogen	Q_1	Q_2	Q_3	Q_4	average	average	average	high	low
Needle blight	−.55*	−.45	−.40	−.55*	−.43	−.63*	−.51*	−.14	−.44
Needle cast	−.04	.12	.10	.13	.02	−.09	.10	.07	.12
Tip dieback	−.14	−.06	−.11	−.21	−.12	−.08	−.16	.20	−.35
Mold-mildew	−.46	−.49*	−.37	−.41	−.52*	−.47*	−.46	−.38	−.15
Galls-foliage	.07	−.11	.00	.14	−.09	.18	.04	−.37	.41
Galls-branch	−.27	−.32	−.24	−.20	−.33	−.19	−.26	−.64*	−.09
Witch's broom	−.43	−.55	−.41	−.45	−.56*	−.34	−.50*	−.56*	−.18
Lesions-foliage	−.30	−.34	−.44	−.33	−.38	−.22	−.33	−.26	−.23
Lesions-branch	−.65**	−.55*	−.37	−.47*	−.43	−.54*	−.51*	−.63**	−.29
Rot-twigs	−.21	−.05	−.09	−.11	−.16	−.50*	−.13	−.13	−.14
Rot-trunk	−.48*	−.38	−.25	−.39	−.37	−.39	−.39	−.06	−.30
Mistletoe	.10	.04	.13	.14	.13	.11	.13	−.29	.15
Insect borers	−.47*	−.21	−.12	−.38	−.16	−.56*	−.33	−.09	−.48*
Scale insects	−.22	−.29	−.36	−.30	−.31	−.30	−.29	−.38	−.19
Insect galls	.19	.20	.15	.12	.34	.41	.17	.35	−.09

* Significant at .05 level
** Significant at .01 level

TABLE 6. Correlations between *J. osteosperma* diseases and insects and precipitation (p) and the four different time quarters (Q).

Pathogen	P Q_1 High	P Q_2 High	P Q_3 High	P Q_4 High	P Q_1 Low	P Q_2 Low	P Q_3 Low	P Q_4 Low	Average annual precipitation
Needle blight	−.71**	−.38	.02	−.09	−.26	.10	.68**	−.00	−.46
Needle cast	−.00	−.22	−.21	.34	.39	−.19	.10	−.37	−.27
Tip dieback	−.44	−.13	−.20	−.29	−.34	.01	.04	.19	−.25
Mold-mildew	−.19	−.31	.02	.58*	−.05	−.05	.47*	−.29	−.09
Galls-foliage	.80**	.34	.31	.67**	.30	.12	−.10	−.11	.75**
Galls-branch	.40	−.15	.67**	.40	−.21	−.13	.14	.09	.53*
Witch's broom	.35	−.08	.64**	.53*	−.05	.04	.25	.05	.57*
Lesions-foliage	−.03	−.12	−.02	.32	.49*	−.04	.18	−.19	−.15
Lesions-branch	−.09	−.52*	.25	.47*	−.10	−.44	.34	.11	.06
Rot-twigs	−.42	−.51*	.05	.13	−.02	−.27	.42	−.25	−.53*
Rot-trunk	−.29	−.38	−.14	.43	.02	−.20	.18	−.14	−.21
Mistletoe	−.03	−.22	.08	.29	−.11	−.29	.03	−.31	−.07
Insect borers	−.89**	−.79*	−.03	−.22	−.63**	−.40	.46	.01	−.71**
Scale insects	−.38	−.18	.23	−.09	−.18	.19	.61**	−.10	−.22
Insect galls	−.02	.22	−.47*	−.38	−.12	−.04	−.39	.16	−.03

* Significant at .05 level
** Significant at .01 level

decayed areas and fruiting bodies. Only tentative identifications of the species were made. Fourteen sites contained trees with wood rot (2–64 trees/transect). The incidence of unidentified fungal diseases on the foliage (mold-mildew) was very similar (Figs. 7, 8) to that of the wood-rotting fungi. These mold-mildew fungi may be similar to those recorded by others (Hodges 1962, USDA Index of Plant Diseases 1960, Horst 1979), i.e., *Cercospora* spp., *Stigmina* spp., *Phoma* spp., *Dimerium* spp., etc. We observed the symptoms of leaf-tip burn, shoot-tip dieback, leaf-needle blight, and needle cast but did not establish specific causal agents for these diseases.

Distinct negative correlations existed between the amount of mold-mildew occurring in a site and temperatures at the site ($\alpha = 0.05$ with spring and summer temperatures) and definite positive correlations between the amount of mold-mildew and the amounts of summer ($\alpha = 0.01$) and fall ($\alpha = 0.05$) precipitation. This corresponds to behavior of foliage pathogens (such as phomopsis, cercospora blight, etc.) in which moderate temperatures

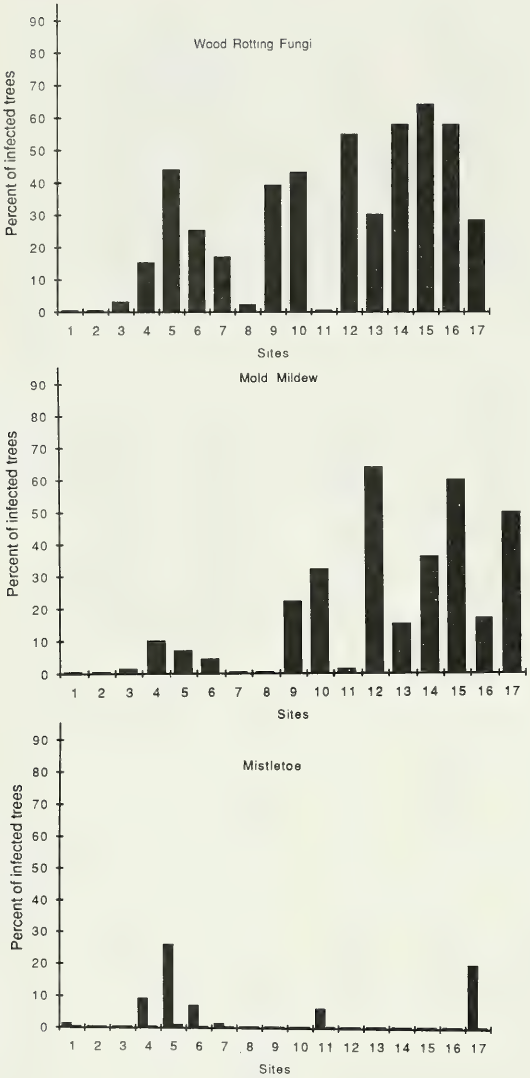

Fig. 5. The percent of trees (*Juniperus osteosperma*) infected with wood-rotting fungi (top), mold mildew (middle), and mistletoe (bottom).

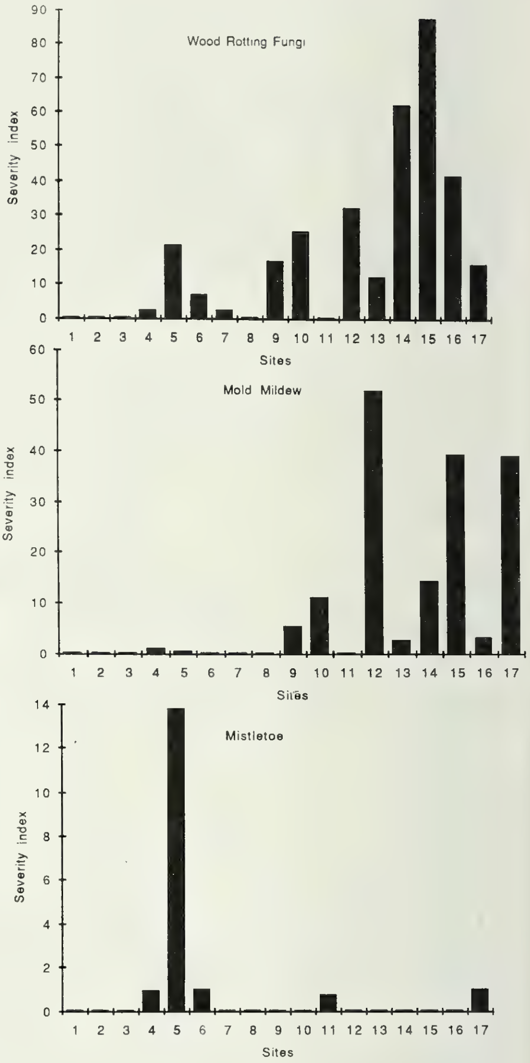

Fig. 6. The severity index of wood-rotting fungi (top), mold mildew (middle), and mistletoe (bottom) on *Juniperus osteosperma* trees.

and high amounts of relative humidity and/or free moisture favor infection. Incidence of wood-rotting fungi seems to be correlated with low winter temperatures ($\alpha = 0.05$), and no correlations exist with amounts of precipitation. There is, however, high correlation with the incidence of wood-rotting fungi in the host and variations in amounts of soil nutrients. If the nitrogen supply to the host is relatively low, the frequency of wood-rotting fungi on the host is greater ($\alpha = 0.05$).

Parasitic Higher Plants

True mistletoe (*Phoradendron juniperium*) Englm. has been reported on Utah juniper in Utah by Hawksworth and Wiens (1966) and in Arizona by Hreha (1978). We found *Phoradendron juniperium* in seven of our transects (Figs. 5, 6).

Injuries of Unknown Origin

A third disease category was designated as injuries of unknown origin. Diseases in this

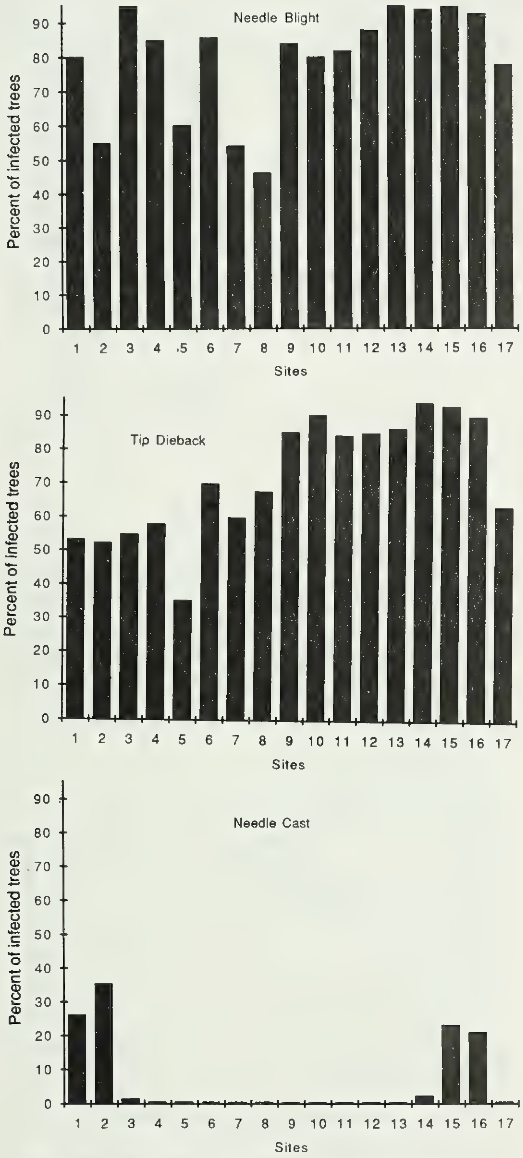

Fig. 7. The percent of infected trees (*Juniperus osteosperma*) with needle blight (top), tip dieback (middle), and needle cast (bottom).

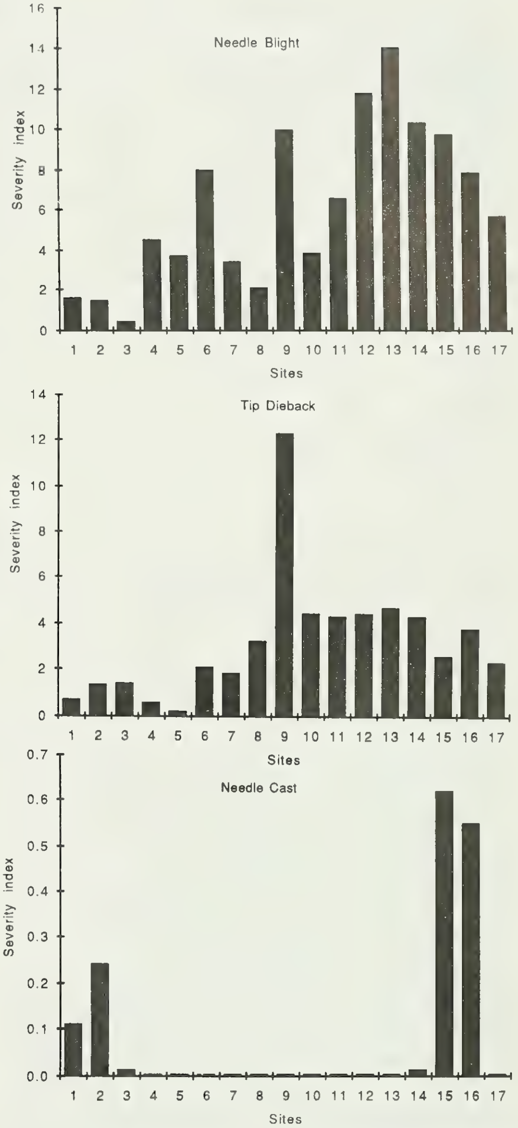

Fig. 8. The severity index of three diseases: needle blight (top), tip dieback (middle), and needle cast (bottom) on *Juniperus osteosperma* trees.

category had symptoms similar to the tipburn, tip-dieback, needle blight, needle cast, and general chlorosis (Figs. 5, 6, 7, 8). Environmental factors such as desiccation, winter injury, high temperature, and nutrient imbalances could cause these injuries. Since some could also be induced by biotic agents, however, we classified them as being of unknown origin. Isolates from these tissues produced a variety of fungi, most of which were probably saprophytes. Although a variety of fungi were isolated from these tissues, their pathogenicity was not established. Consequently, no specific cause was assigned for these diseases.

It was possible, however, to separate injuries into three groups (Figs. 7, 8) as was done earlier by Horst (1979). Symptoms of needle blight and tip dieback occurred at every site, and needle-cast was observed on approximately one-third of the sites.

TABLE 7. Correlations between *J. osteosperma* diseases and insects versus soil variables.

Pathogens	pH	ECx10^3	%N	ppm P	ppm K	ppm Ca
Needle blight	.31	.51*	−.37	−.12	.20	−.52*
Needle cast	.21	−.12	−.10	−.24	−.01	.32
Tip dieback	.31	.26	−.08	.66**	.43	−.04
Mold-mildew	.09	.01	−.47*	−.27	.28	.08
Galls-foliage	−.32	−.34	.07	−.19	−.39	.41
Galls-branch	−.21	−.13	−.33	−.22	−.34	.27
Witch's broom	−.15	−.18	−.43	−.18	−.20	.17
Lesions-foliage	.49*	−.07	−.15	−.17	.12	.02
Lesions-branch	.15	−.08	−.70**	−.47*	−.03	−.02
Rot-twig	.26	.11	−.22	−.38	.07	−.03
Rot-trunk	.20	−.08	−.57*	−.20	.48*	−.02
Mistletoe	−.23	−.11	−.20	−.33	.11	−.19
Insect borers	.29	.24	−.62**	−.18	.49*	−.29
Scale insects	.23	.54*	−.16	−.22	−.03	−.34
Insect galls	.30	−.24	.18	.56*	.44	.31

* Significant at .05 level
** Significant at .01 level

The incidence of needle blight was the most responsive of the three diseases to variations in the environmental factors we measured. Incidence was consistently negatively correlated ($\alpha = 0.05$) with sites that had low temperature periods throughout the year, and particularly for the low winter temperatures ($\alpha = 0.01$). The correlation with precipitation was similar. Needle blight was more intense in those sites with the lowest winter precipitation ($\alpha = 0.05$). Incidence of needle blight was positively correlated with summer drought ($\alpha = 0.01$). These results suggest that environmental stress contributes significantly to this symptom, and it may be the result of desiccation or winter injury. The pinyon-juniper woodlands rely heavily on winter precipitation to replenish soil moisture since precipitation in other periods of the year is sporadic. In areas where soil reserves are marginal, moisture deficits during hot summer months may produce the symptoms we observed.

The incidence of needle blight was also correlated with two soil factors (Table 7). Sites with a higher soil salinity as measured by the electrical conductivity (EC) had higher percentages of trees with needle blight. That this may be a direct response is supported by previous work (Bunderson 1983) in which small elevations in the amount of EC in the soil were correlated with lower concentrations of total chlorophyll in the foliage of Utah juniper. The amount of total soluble carbohydrate in the foliage increased with higher EC in the soil, which may indicate a decrease in the metabolic efficiency of the plant. The correlation ($\alpha = 0.05$) of needle blight with the amount of calcium in the soil indicates that, when calcium is relatively plentiful, the percent of needle blight on the site is lower, and we hypothesize that as soil calcium content increases, the detrimental effect of salinity on Utah juniper is ameliorated.

Tip dieback, while also having a moderate negative correlation with low winter precipitation, has no correlation with temperature. Contrary to expectations, tip dieback was more common on trees with higher nitrogen levels in the foliage ($\alpha = 0.05$) and higher phosphorus ($\alpha = 0.01$) and potassium ($\alpha = 0.10$) levels in the soil. Until fungi can be associated with these symptoms and pathogenicity established, relationships to other factors remain speculative.

Gymnosporangium Rusts

The most frequent juniper pathogens we encountered on our research sites were the *Gymnosporangium* rust fungi. These rust fungi are parasitic and most are heteroecious. The alternate hosts of *G. inconspicuum* and *G. kernianum* are species of *Amelanchier*, most commonly *A. utahensis* Koehne. (*A. alnifolia* Nutt. is also a frequent alternate host for *Gymnosporangium* rusts, although usually for those species that parasitize Rocky Mountain juniper (*Juniperus scopulorum* (Sarg.) rather than *J. osteosperma*). *Gymnosporangium nelsoni* has been found on *Amelanchier* and, locally, on *Peraphyllum ramos-*

ppm Mg	ppm Na	ppm SO-S	ppm Fe	% Sand	% Silt	% Clay
−.06	−.25	.24	.17	−.21	−.24	−.20
.23	.24	.07	−.28	−.04	−.09	.26
.27	−.27	.27	.29	−.23	−.27	.11
.18	−.01	.00	−.22	.04	−.06	.07
.09	.45	−.49*	−.28	.48*	.42	.31
−.02	.37	−.24	−.04	.39	.01	.20
.16	−.09	−.45	−.09	.54*	.27	.35
.20	−.16	.24	−.04	−.24	−.21	.18
.13	−.05	−.30	−.48*	.46	.05	.13
−.04	.25	.45	.11	−.34	−.52*	−.08
.31	−.47*	−.22	−.35	.26	.13	.12
−.38	.13	−.11	−.27	.23	−.07	−.48*
.01	−.21	.18	−.03	−.03	−.35	−.20
−.30	.28	.45	.26	−.43	−.40	−.31
.56*	−.13	−.30	−.04	.22	.35	.22

sissimum Nutt. The alternate hosts of *G. speciosum* have been reported on species of *Fendlera* and *Philadelphus* (Kern 1973).

In our transects the incidence of rust on juniper was not significantly correlated with the frequency and close proximity of the alternate host. This was not unexpected considering the differing ecological habitats of *Amelanchier* and *Juniperus* species. Since basidiospores are capable of traveling considerable distances and remaining viable (Parmelee 1968), and because aeciospores may remain viable as long as one year (Miller 1932), alternate hosts need not to be in close proximity for infection of either to occur.

Temperature and moisture requirements for the release of *Gymnosporangium* basidiospores have been well documented by Pearson et al. (1980), Pady and Kramer (1971), and Pearson et al. (1977). Although little is known about the specific requirements for infection of juniper, it is obvious that these requirements were met in our research sites (Table 8). *Gymnosporangium speciosum* and *G. kernianum* were less widespread than either *G. inconspicuum* or *G. nelsoni*. Peterson (1967) noted that *G. kernianum* is absent from many stands throughout the Great Basin where both hosts occur together. Our data support this observation.

A Predictive Model

Disease occurrences are determined by complex environmental interactions and causal agents. In the present study we have used descriptive data to develop hypotheses for correlating the incidence of disease with climate, soil, and other site factors in Utah juniper habitats.

Distributions of several of the disease variables were sufficiently peaked or had such high degrees of skewness that the populations did not fit the normal distributions that are implicit in correlational or factor analyses. Even though the correlations in our study are unusually stable because of the size of our data base (96 trees in each of 17 sites), nonparametric methods of analysis were used to generate predictive models from our data.

We applied the weighted least squares analysis for categorical data (Forthofer and Lehnen 1981). Using the environmental variables that generally encourage the growth and proliferation of fungi causing mold and/or mildew symptoms, the following hypotheses were generated:

1. High amounts of fall precipitation characterize sites with high amounts of mold-mildew on the foliage.
2. Low summer temperatures characterize sites with high amounts of mold-mildew on the foliage.
3. High nitrogen nutritional status of the plant is conducive to low amounts of mold-mildew on the foliage.

Five of the 17 sites were selected, each of which contained trees infected with a mold/mildew pathogen. Each of these sites also differed from the others on the three environmental variables chosen to formulate the three hypotheses. The hypotheses can be reflected as linear weights where:

TABLE 8. Correlations between *J. osteosperma* diseases and insects and site characteristics.

pathogen	Distance	Height	Diameter	Age	Soil depth
Needle blight	−.45	−.45	−.13	.24	−.38
Needle cast	.54*	−.21	.20	.08	−.33
Tip dieback	−.23	−.39	−.13	.12	−.30
Mold/mildew	−.17	−.02	.21	.21	−.34
Galls-foliage	.43	.66**	.05	−.26	.24
Galls-branch	.16	.48	−.10	−.15	−.02
Witch's broom	.19	.47*	.22	.15	.07
Lesions-foliage	.17	−.41	.06	−.05	−.53*
Lesions-branch	−.29	.41	.28	.53*	−.02
Rot-twig	.13	−.41	−.14	.10	−.55*
Rot-trunk	−.27	.09	.61**	.69**	−.03
Mistletoe	−.41	.20	−.16	−.02	.08
Borers	−.57*	−.27	.01	.55*	−.30
Scale insects	−.25	−.63**	−.67**	−.55**	−.59**
Insect galls	.02	.12	.11	−.05	.19

* Significant at .05 level
** Significant at .01 level

1 = The hypothesis is true for this site.
−1 = The hypothesis is not true for this site.
0 = This site was not considered when making this hypothesis.

These weights were entered into the following X matrix where row 1 is equivalent to site 5, row 2 to site 6, row 3 to site 9, row 4 to site 14, and row 5 to site 15.

X Matrix:

Row 1	1	0	1	1
Row 2	1	0	1	0
Row 3	1	1	−1	0
Row 4	1	0	−1	−1
Row 5	1	−1	−1	1

Column 1 represents the presence or absence of mold/mildew at each of the selected sites. Since each site was selected because mold/mildew was present, column 1 is a constant. Column 2 represents the linear weights of hypothesis 1; column 3, hypothesis 2; and column 4, hypothesis 3. From this matrix of linear weights based on our hypotheses, we have predicted the incidence of mold-mildew at sites 5, 6, 9, 14, and 15. The predicted and observed occurrences of mold/mildew expressed as proportions of infected trees are presented below. From the small residual figures, the success of the three hypotheses at predicting the proportion of infection seems good.

Site	Observed	Predicted	Residual
5	.073	.074	−.001
6	.042	.041	.001
9	.229	.228	.001
14	.375	.377	−.002
15	.625	.624	.001

The overall chi^2 (X^2) goodness of fit for the observed versus predicted data was 0.004, and the beta weight for the matrix constant (column 1) was 0.226. The beta weights for each of the hypotheses were −0.181, −0.184, and 0.033. The very small chi^2's and the small residual values indicate an excellent fit for the hypothetical model to the observed incidence of mold-mildew. The hypotheses were tested for significance of the X^2 values:

Hypothesis 1 = 27.7
Hypothesis 2 = 126.3
Hypothesis 3 = 1.6

Significance of X^2 values:

.05 level 3.84
.01 level 6.63
.001 level 10.83

Using this procedure we can affirm that high amounts of fall precipitation and low summer temperatures do indeed characterize sites with high amounts of mold-mildew on Utah juniper foliage. The first two hypotheses of our model have reliably predicted the proportion of trees in a pinyon-juniper site that could be expected to be infected with mold-mildew. The third hypothesis was not confirmed.

As can be seen from the predictive ability of the generated hypotheses and the power to statistically confirm their validity, such a nonparametric statistical model offers a valuable tool for understanding the interactions between the many variables that exist in any ecosystem.

Vigor	Decadence	Density	Slope	Elevation	Exposure	Alternate host
.38	.22	.32	−.21	.33	−.20	−.09
−.01	.09	−.53*	−.20	−.03	.05	.25
.36	.04	.10	.05	.12	−.25	−.05
−.07	.64**	.08	.05	.52*	−.37	.34
−.56**	.16	−.31	.01	.04	−.10	.27
−.45	.16	−.16	.19	.54*	−.06	.51*
−.67**	.55*	−.19	.06	.49*	.04	.39
.02	.05	−.14	−.14	.17	.31	.39
−.40	.55	.25	.08	.60**	.17	.37
.29	.03	−.19	.00	.15	−.30	.13
−.34	.89**	.27	.02	.34	.06	.33
−.07	.10	.58*	.05	.37	.01	.44
.30	.33	.45	.18	.51*	−.12	.12
.60**	−.40	.20	−.14	.44	−.11	.21
.16	−.21	−.18	.48*	−.19	.09	−.08

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STATUS AND DISTRIBUTION OF THE FISH CREEK SPRINGS TUI CHUB, *GILA BICOLOR EUCHILA*

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ABSTRACT.—The Fish Creek Springs tui chub, *Gila bicolor euchila*, is present in large numbers throughout its native habitat in spite of extensive man-caused habitat disturbance. This subspecies occurs further downstream in Fish Creek than previously reported.

The Fish Creek Springs tui chub *Gila bicolor euchila* was described by Hubbs and Miller (1972) as an endemic subspecies restricted to the springs and outflows of Fish Creek Springs in southeastern Eureka County, Nevada, in R.53E., T. 16N., S. 8 and 9 (USGS Bellevue Peak Quadrangle 1956). Subsequently, Hardy (1979a, b) found this subspecies in only one spring and failed to find any in the outflows. In 1983 (Federal Register 1984), the fish was reported from three springs, but not from the outflows, and was proposed for listing as "threatened" with critical habitat designated under 50 Code of Federal Regulations Part 17.

METHODS AND MATERIALS

Parts of the present habitat of *G. b. euchila* were sampled on 9–10 July 1984 and 26–27 June 1985. Unbaited 6-mm wire mesh, Gee-type minnow traps were used. Catch and total-length data are presented in Table 1. Some physical and chemical characteristics of this system are reported in Table 2. Temperature was measured with a standard mercury bulb thermometer, and pH was measured with a Hach High Range pH test Cube No. 12519-00. Conductivity was measured with a Lab-Line Lectro MHO-Meter, Model MC-1, Mark IV and is reported in Micromhos/cm. In 1985 dissolved oxygen was measured with a Hach Portable Dissolved Oxygen Meter.

RESULTS

The Fish Creek Springs system is composed of two isolated northern spring-pools and a number of other springs connected by channelized outflows (Fig. 1, Sites 13–14). In 1938, and at least until 1956, the two northern springs were connected by outflow to the remainder of the system (Hubbs et al. 1974). The combined outflows form Fish Creek, which passes just south of Fish Creek Ranch and terminates in a reservoir about 1 km east of Nevada State Route 20.

Man-caused modification of this system has occurred frequently in the past. For example, Hubbs et al. (1974) report that in 1938 Fish Creek was dry where it crossed Nevada State Route 20 because of water consumption on Fish Creek Ranch.

Prior to our 1984 survey, a dragline had been used to clear Fish Creek throughout sections 9 and 10. In 1984 the westernmost spring (map reference 1) was little more than a muddy swale with a diameter of about 15 m and an area of dense rushes (*Juncus* sp.) in the middle. Water, however, continued to flow from this spring into an outflow stream about 300 m long (map reference 2) into the main body of the aquatic system. By 1985 the spring-pool had been cleaned of emergent aquatic vegetation and deepened and was, essentially, an open body of water. By 1985 heavy equipment had been used to dredge almost all the spring-pools and their outflow channels. Emergent aquatic vegetation was reduced throughout the system by about 75% compared to 1984. Dredged material was placed in piles alongside most of the spring-pools and outflows.

Gila bicolor euchila presently occurs in large numbers in most components of this system (Table 1). In addition, it was found in

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TABLE 1. Catch and total length (TL) data for *Gila bicolor euchila* from Fish Creek Springs, 1984–1985. Numbers in parentheses represent the number of fish measured.

Map #	Trap-hours	Fish caught	Catch per trap-hour	$\bar{x}$ Total [(N) = fish measured] length—mm	Total length range—mm
1984					
2	15	64	4.3	(64) 50.4	31– 64
3	4	1	0.3	105.0	—
5	2	76	38	(50) 46.3	32– 78
6	1	30	30	(30) 63.0	44– 78
9	1	28	28	(28) 54.5	38– 68
10	1	19	19	(17) 54.9	43– 74
13	9	120	13.3	(75) 64.0	38–113
14	3	0	0	0	0
15	14	8	.6	(8) 74.3	40–122
16	10	4	.4	(4) 61.8	45– 84
1985					
2	6	86	14.3	(50) 59.9	41– 77
5	2	126	63.0	(50) 64.9[1]	46–122[1]
6	2	106	53.0	”	”
13	17.5	277	15.8	(100) 77.3	33–118

[1] Sites 5 and 6 combined.

TABLE 2. Physical and chemical characteristics of the Fish Creek Springs system, 1984–1985.

Map #	Area type	Temperature C	pH	Conductivity micromhos	Dissolved oxygen ppm
1984					
2	outflow-stream	—	8.0	505	—
3	spring-pool	22	7.5	500	—
4	spring-pool	—	—	550	—
5	spring-pool	—	7.0	—	—
9	spring-pool	—	7.0	530	—
10	outflow-stream	—	7.5	540	—
13	spring-pool	21.5	8.0	570	—
14	spring-pool	26.0	8.0	594	—
15	canal	11.0	8.5	420	—
1985					
2	outflow-stream	23.8	8.0	618	15.4
5	spring-pool	17.2	7.0	617	6.3
13	spring-pool	16.2	7.6	557	8.5

the outflow of Fish Creek Springs in the southern portion of section 10 closely adjacent to the Fish Creek Ranch headquarters. This is beyond the range reported for this subspecies by Hubbs et al. (1974) and in the Federal Register (1984). In 1984 this subspecies was also taken in section 12 at the intersection of the outflow with Nevada State Route 20. Fish were also seen but not captured about 50 m downstream from this intersection in 1985. This area is about 4.8 km east of the previous easternmost record for this subspecies (Federal Register 1984). Visual inspection of the remainder of Fish Creek down to and including the reservoir revealed no fish.

In 1984 a total of 350 fish were captured from 10 trap sites beginning in section 8 and terminating in section 12. Of the fish captured, 276 were measured (Table 1). In 1985, 595 fish were captured from four sites, and 200 of these fish were measured (Table 1). Thousands of fish ranging from about 5 mm

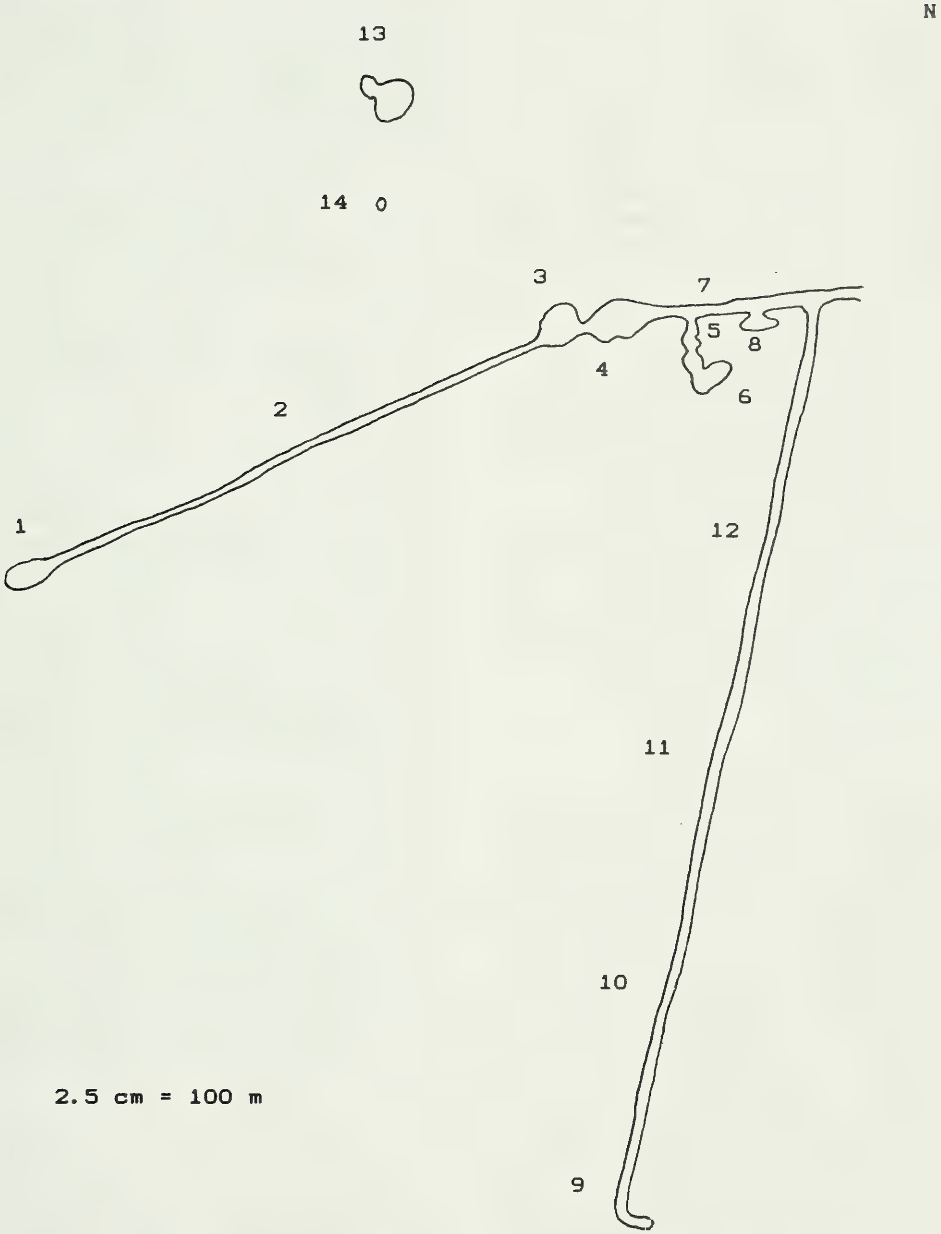

Fig. 1. General configuration of Fish Creek Springs and outflow. Numbers indicate the location of various components of the system within section 8. Sampling site 15 is in section 10, and sampling site 16 is in section 12; neither are shown here. Elevation of the westernmost spring (site 1) is 6,040 ft. It and the northernmost spring (site 13) joined near site 3 on the Bellevue Peak Quadrangle (1956) in 1938.

(TL) to more than about 150 mm were seen during visual inspections of the spring system in both 1984 and 1985. No other fish species were seen or trapped in either 1984 or 1985; however, Hubbs et al. (1974) report that rancher Isador Sara planted both rainbow trout (*Salmo gairdneri*) and brook trout (*Salvelinus fontinalis*) as early as about 1934, and Pat Coffin (Nevada Department of Wildlife, personal communication) reports that rainbow trout (*Salmo gairdneri*) are planted in the springs each spring. The Federal Register (1986) states that 7,000 "catchable-sized" brown trout, *Salmo trutta*, were planted in Fish Creek Springs in 1973, 1976–1978, and 1981 and notes that the increase in tui chub numbers "corresponds with the cessation of brown trout stocking in the springheads".

Trap results and length measurement data for map reference areas 2, 3, 6, 10, 13, 15, and 16 (1984) and 2, 5, 6, and 13 (1985) are presented in Table 1. Catch per trap-hour ranged from .3 to 38 in 1984 and 14.3 to 63.0 in 1985. The total length (TL) range from all sites in which fish were taken in 1984 was from 31 mm to 122 mm ($\bar{x} = 54.8$) and in 1985 from 33 to 122 mm ($\bar{x} = 69.8$). Catch per trap-hour was greater at all the sites sampled in 1985 than at the same sites sampled in 1984.

Table 2 presents some of the physical and chemical characteristics of the areas referred to in Figure 1. Water temperature ranged from 11 to 26 C, pH from 7.0 to 8.5, conductivity from 420 to 680 micromhos, and dissolved oxygen from 6.3 to 15.4 ppm.

SUMMARY

The aquatic system at Fish Creek Springs is composed of a number of springs and their outflows. Human modification of the site includes dredging of the spring-pools and their outflow channels, cattle grazing, and introductions of trout. Even with extensive modification of the natural system, *Gila bicolor euchila* is present in large numbers in most components of the system. The presence of these fish in sections 10 and 12 extends the range of this subspecies about 4.8 km east of localities previously reported. Fish numbers appear to have increased following 1981 when *Salmo trutta* was last planted in the Fish Creek Springs system.

ACKNOWLEDGMENTS

We thank the U.S. Fish and Wildlife Service and the Nevada Department of Wildlife for their financial support of this project. Suzanne Pedretti assisted in the field during the 1985 survey.

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PONDEROSA PINE CONELET AND CONE MORTALITY IN CENTRAL ARIZONA

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ABSTRACT.—Ponderosa pine conelets in 10 stands on the Coconino and Kaibab national forests were observed periodically from July 1982 until they matured in September 1983. Abortion, ponderosa pine cone beetles (*Conophthorus ponderosae* Hopkins), and ponderosa pine coneworms (*Dioryctria* sp., probably *Auranticella* [Grote]) were the significant mortality factors. Cattle, tip moths, and squirrels rarely destroyed conelets or cones.

Good cone crops in stands of ponderosa pine, *Pinus ponderosa* Lawson, in the Southwest occur on the average of every three to four years (Schubert 1974), with large crops about every five years (Larson and Schubert 1970). Because good cone crops occur infrequently and natural regeneration is difficult to obtain, any factor adversely influencing cone production, and therefore seed production, needs to be identified. Cone mortality is caused by insects, small mammals, and weather factors (Schubert 1974). Cone beetles (*Conophthorus*) have occasionally destroyed 50% of the cone crop in some locales (Pearson 1950). Mice, chipmunks, and ground squirrels may eat seeds but are not important while the cones are attached to the branches. Abert squirrels, *Sciurus aberti* Woodhouse, on the other hand, destroyed an average of 20% of the cone crop over a 10-year period (Larson and Schubert 1970). Freezing temperatures in June have also killed conelets (Schubert 1974).

This paper reports on the conelet and cone mortality caused by different factors during a two-year period.

METHODS

Ten cone-producing areas were selected in ponderosa pine stands on the Coconino and Kaibab national forests in north central Arizona (Fig. 1). For an area to be selected, it had to have 10 trees bearing conelets. In most areas, each tree usually bore more than 30 conelets, but only 30 conelets were randomly selected for study. In one area, Dutch Kid, each tree had less than 15 conelets, so only 10 were selected. Two other areas, Devil Dog and Ten-X, had individual trees with fewer than 30 available cones, so the desired number of 300 conelets per area was not attained. Table 1 shows the total number of conelets observed per area.

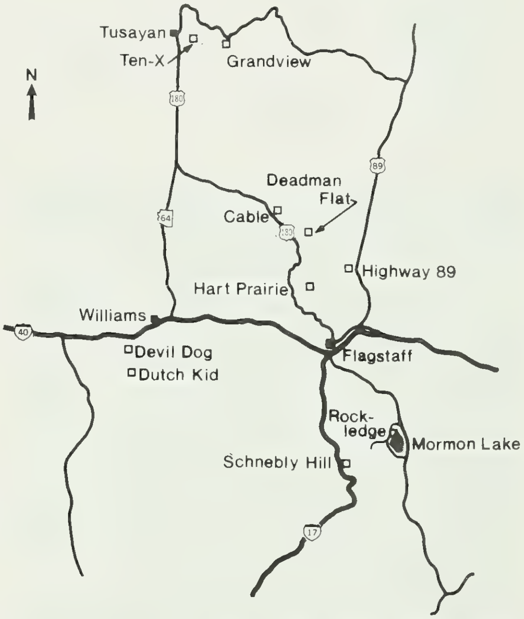

Fig. 1. Location of study areas on the Coconino and Kaibab national forests, Arizona.

The conelets were generally on the lower crown branches of large-diameter, open-grown trees. The conelets were randomly selected from those within 4 m of ground level because no equipment was available to examine cones above that height. Conelets were present individually and in clusters of two to

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TABLE 1. Number of ponderosa pine cones observed in each area, Arizona 1982–1983.

National forest/Area	Number of cones	Elevation
		m
Coconino National Forest		
Cable	302	2,226
Deadman Flat	301	2,290
Hart Prairie	301	2,561
Highway 89	301	2,195
Rockledge	300	2,195
Schnebly Hill	300	1,980
Kaibab National Forest		
Devil Dog	281	2,012
Dutch Kid	100	2,012
Grandview	301	2,256
Ten-X	291	2,025

five. Their cone cluster class was recorded to determine whether insect damage varied with the number of cones per cluster.

The conelets were selected in July 1982 and were examined about every two weeks thereafter until September 1982. Observations were discontinued during the winter of 1982–1983 but were begun again in March or April 1983, depending on accessibility of the site. In August–September 1983 observations were terminated and the cones collected for additional study. During each observation period, factors causing damage or mortality were identified when possible.

Some of the areas were the same as those used by Schmid et al. (1984) in an earlier study, in which 32 cones were collected from the lower and middle crowns of large-diameter, open-grown trees in September 1982. However, in that study cones were not observed from the time they were conelets.

RESULTS AND DISCUSSION

Abortion, ponderosa pine cone beetles (*Conophthorus ponderosae* Hopkins), and ponderosa pine coneworms (*Dioryctria* sp., probably *D. auranticella* Grote) were the three most important mortality factors, with abortion consistently causing the greatest amount of conelet mortality (Table 2). Abortion, as used herein, encompasses several mortality factors. Conelets died and failed to mature, but the exact cause of their death was undetermined. Many of the conelets died the first summer, which suggests some physiological disfunction, i.e., inadequate pollination or water stress. The 1983 mortality was primarily observed when observations were resumed, which indicates that the mortality occurred during the winter months. Schubert (1974) and the USDA Forest Service (1974) note cold temperatures can be lethal, so much of the 1983 mortality may be attributed to freezing temperatures. In December 1982 and January and February 1983, temperatures dropped below 0 F in Flagstaff, but whether these low temperatures caused overwinter mortality was not determined. And finally, insects like seedbugs (*Leptoglossus occidentalis* Heidemann) could cause conelet mortality, although neither the adults nor damage were observed. In the life of the cone, mortality factors during the first year are the least understood.

Although *Conophthorus*-caused mortality was 10% or less in 7 of the 10 areas, *Conophthorus* beetles generally caused the second greatest amount of mortality, causing up to 62% mortality in one area (table 2). *Conophthorus*-caused mortality changed significantly between 1982 and 1983 in two locations and remained the same in two other areas. In 1982, *Conophthorus*-caused mortality averaged 39% in the Highway 89 area and 2% in the Ten-X area (Schmid et al. 1984). In 1983, the second year of this study, mortality attributable to *Conophthorus* was 1% in Highway 89 and 28% in Ten-X. Whereas the two studies have slightly different sampling designs, which may have created some of the difference in the incidence of mortality, enough difference exists to suggest that *Conophthorus* populations, and therefore *Conophthorus*-caused mortality, exhibit significant variation from year to year.

The frequency of *Conophthorus*-killed cones mirrored the frequency of the cone cluster class for all levels of *Conophthorus*-caused mortality. When two-cone clusters were the most abundant cone cluster, *Conophthorus* damage was greatest in that class. When three-cone clusters predominated, damage was greatest in that class. Thus, even though female beetles can infest more than one cone (Kinzer et al. 1970), multiple cone clusters do not apparently reduce beetle mortality during dispersal and host location nor do they increase the probability of

TABLE 2. Percent mortality* of developing ponderosa pine cones by location and mortality factors, Arizona 1982–1983.

Mortality factor	Coconino National Forest						Kaibab National Forest			
	Cable	Deadman Flat	Hart Prairie	Highway 89	Rockledge	Schnebly Hill	Devil Dog	Dutch Kid	Grandview	Ten-X
Abortion										
1982	13	15	10	6	5	8	13	10	8	21
1983	15	4	7	7	17	22	15	14	8	13
Total	28	19	17	13	22	30	28	24	16	34
Cattle	0	0	0	0	0	1	0	0	1	0
Conophthorus	<1	14	62	1	3	1	2	<1	10	28
Dioryctria	4	7	1	6	0	1	3	0	5	1
Missing	0	2	2	0	<1	2	3	0	0	0
Rhyacionia	0	<1	0	0	0	0	1	0	0	0
Squirrel	0	1	0	2	1	0	<1	0	<1	0

*Mortality will not add up to 100% because not all cones died or disappeared.

Conophthorus infestation. It also suggests that although females can attack more than one cone, they probably do not do so.

Dioryctria-caused damage averaged 7% or less in all areas. *Dioryctria* averaged 0.5% in 1982 and 4% in 1983 for those areas that were also used in 1982 by Schmid et al. (1984). *Dioryctria* damage was thus significantly greater in 1983, which supports the hypothesis of increasing insect damage in areas where good cone crops are produced consecutively for several years.

Conelet and cone mortality caused by cattle, tip moths, and squirrels was generally rare, averaging less than 1% for each factor. Cattle destroyed conelets on two areas by chewing off the tips of the low branches. Cattle were only important here because conelets in the lower crown were being studied; on a whole-tree basis, cattle were insignificant. Similarly, tip moths (probably *Rhyacionia neomexicana* (Dyar)) caused minimal damage on two areas and on a whole-tree basis were insignificant.

Mortality attributable to squirrels (probably the Abert squirrel) averaged less than 1% (Table 2) but was evident in more areas than mortality caused by cattle or tip moths. Squirrels cut few developing conelets prior to maturation and are thus insignificant predators of ponderosa pine conlets during the development stage. Significant cone loss, as noted by Larson and Schubert (1970), occurs when cones mature in September of the second year or about the time our observations were terminated.

Conelet losses attributed to specific mortality factors were identified during specific time periods. Figure 2 depicts survivorship curves for cones on 3 of the 10 areas (Highway 89, Hart Prairie, Ten-X), each of which exemplifies a different situation. The Highway 89 area had the lowest abortion rate and high cone damage caused by *Dioryctria*. Abortions were evenly divided between 1982 and 1983. *Dioryctria* killed 6% of the cones between 15 May and 15 June; losses thereafter were relatively small. The Hart Prairie area had a low abortion rate and substantial losses caused by *Conophthorus*. After abortion losses in the summer of 1982 and losses in the winter months of 1982–1983, conelet mortality was negligible until *Conophthorus* beetles caused a rapid decline in the percentage of surviving cones between 15 June and 15 August. The Ten-X area had high cone mortality attributable to abortion and *Conophthorus*. Abortion losses were greater in 1982 and 15 April to 15 May 1983 in the Ten-X area than in the Hart Prairie. From 15 June to 15 July, the rate of loss to *Conophthorus* was similar in the Ten-X and Hart Prairie areas, but the total loss of conelets was greater in the Hart Prairie area.

MANAGEMENT IMPLICATIONS

This study showed abortion, cone beetles, and coneworms to be the most important factors affecting cone survival. Losses to abortion cannot be reduced until the specific factors responsible can be isolated and identified as to

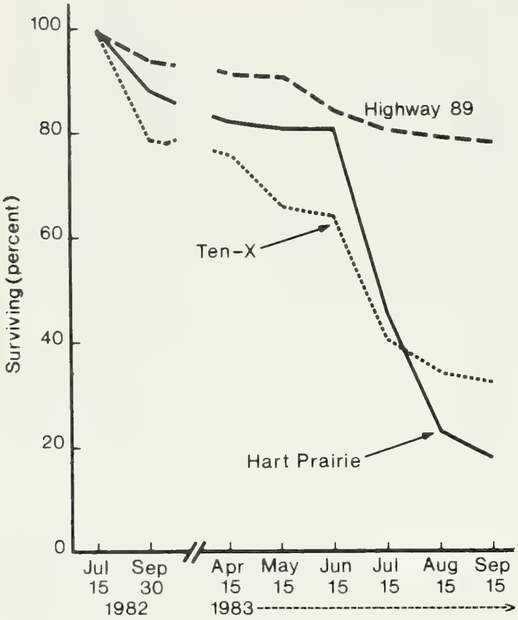

Fig. 2 Ponderosa pine conelet survival for three study areas on the Coconino and Kaibab national forests, Arizona, 1982–1983.

their relative importance. Losses to *Conophthorus* and *Dioryctria* can be drastically reduced using chemical insecticides. If an area produces a good conelet crop and seed is needed from it, a preventive spray might be applied in May or early June of the year the cones mature to keep these cone beetles and coneworms from infesting the cones.

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NUMBER AND CONDITION OF SEEDS IN PONDEROSA PINE CONES IN CENTRAL ARIZONA

J. M. Schmid[1], S. A. Mata[1], and J. C. Mitchell[1]

ABSTRACT.—Ponderosa pine cones from 10 areas in Arizona were collected prior to natural seed dispersal and dissected to determine the number of sound, hollow, and insect-damaged seeds in each cone. Total and sound seed yields per cone did not vary significantly among areas but did vary significantly among trees within each area. Numbers of hollow and *Megastigmus*-infested (Hymenoptera: Torymidae) seeds varied significantly among areas and trees within areas. Numbers of sound seed increased significantly with increasing cone length but did not change with increasing numbers of cones per cluster. The percentages of *Megastigmus*-infested seed did not change significantly with increasing cone length or number of cones per cluster.

Good cone crops are the first step in obtaining natural regeneration in stands of ponderosa pine, *Pinus ponderosa* Douglas ex Lawson. Good cone crops occur every three to four years (Schubert 1974), with exceptional crops every five years (Larson and Schubert 1970). Good to exceptional cone crops, however, do not insure good to exceptional sound seed yield. Cone crops can be substantially destroyed by insects (Schmid et al. 1986), or seed within the cones can be damaged or destroyed so that sound seed yield is substantially lessened. Seed chalcids may destory 77% of the seed in some instances (Schmid et al. 1984), and other insects and physiological impairments may further reduce sound seed yield. This note reports on the total, sound, hollow, and insect-damaged seed from 10 areas in Arizona.

METHODS

Ten areas with first-year conelets were selected on the Coconino and Kaibab national forests in Arizona in July 1982 (Schmid et al. 1986). Trees with conelets were generally more than 18 inches dbh and 50 feet tall in 8 of the 10 areas. In the other 2 areas, trees were 8–12 inches dbh and 20–45 ft tall. On all sites the trees were open-grown, and stand density was less than 50 square feet of basal area per acre.

Ten trees were selected in each area, and at least 30 conelets were tagged on each tree in 9 of the 10 areas. In the tenth area fewer than 15 conelets were available on each tree, so only 10 per tree were tagged. Conelets were present individually and in clusters of two to five. All tagged conelets were within 12 feet of ground level, so they could be observed from the ground or from a stepladder. The conelets were observed periodically during the summers of 1982 and 1983. In September 1983 all tagged live cones on each area were picked (Table 1) and taken to the laboratory. Each cone was measured lengthwise, then dissected to determine the number of sound, hollow, insect-damaged, and total seeds. Sound seeds had white endosperm completely filling the seedcoat. Hollow seeds were without contents or had a shriveled remnant inside the seedcoat.

Mean numbers of each seed category per cone were calculated for each area on a per tree basis. Numbers of each category per cone were tested by nested analysis of variance for significant differences among areas and among trees within areas, $\alpha = 0.05$. Percentages of each seed category were also tested by analysis of variance for significant variation associated with cone length and the number of cones per cluster, $\alpha = 0.05$. When significant differences were indicated, Tukey's multiple range test was used to determine which mean values were significantly different from each other.

RESULTS AND DISCUSSION

Total Seeds

Mean number of total seeds per cone per area ranged from 47 to 68 (Table 1) and was not

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TABLE 1. Number of cones dissected and mean number of total seeds per cone per tree within each area, Arizona 1983.[1]

National forest/Area	Number of cones	$\bar{x}$ ± S.D.	Range
Coconino National Forest			
Cable	199	67 ± 24a	21- 92
Deadman Flat	176	56 ± 15a	22- 72
Hart Prairie	53	61 ± 19a	41-100
Highway 89	230	68 ± 16a	46- 89
Rockledge	214	56 ± 16a	33- 83
Schnebly Hill	140	52 ± 14a	30- 72
Kaibab National Forest			
Devil Dog	173	59 ± 22a	25- 94
Dutch Kid	66	56 ± 15a	24- 74
Grandview	194	47 ± 8a	31- 56
Ten-X	99	50 ± 14a	30- 68

[1] Means followed by the same letter are not significantly different, $\alpha = 0.05$.

TABLE 2. Mean number of sound, hollow, and *Megastigmus*-infested seeds per cone per tree by area.[1]

National forest/Area	Sound	Hollow	*Megastigmus*
		$\bar{x}$ ± S.D.	
Coconino National Forest			
Cable	49 ± 23a	16 ± 5cd	0.4 ± 0.7a
Deadman Flat	40 ± 13a	6 ± 2ab	8 ± 1 b
Hart Prairie	58 ± 19a	3 ± 2a	0.2 ± 0.5a
Highway 89	50 ± 17a	16 ± 14cd	2 ± 2 a
Rockledge	46 ± 17a	7 ± 4abc	2 ± 2 a
Schnebly Hill	35 ± 11a	12 ± 7abcd	3 ± 3 a
Kaibab National Forest			
Devil Dog	42 ± 20a	16 ± 8bcd	0.6 ± 1 a
Dutch Kid	38 ± 15a	19 ± 11d	0 a
Grandview	42 ± 8a	4 ± 1a	7 ± .6a
Ten -X	37 ± 12a	12 ± 3abcd	< .1 ± .1a

[1] Means within the same column followed by the same letter are not significantly different, $\alpha = 0.05$.

significantly different among areas. The mean number of seeds per cone per area was generally greater in 1983 than in 1982 for those areas common to an earlier report (Schmid et al. 1984) and this study.

The mean number of total seeds per cone per tree varied significantly in all areas and accounts for the large variation in the range of mean number of seeds per area. Why some trees produce 20 to 30 seeds per cone whereas others produce 80 to 90 is unknown. Competition between adjacent trees was not important because the trees were widely spaced and open-grown.

Total seeds per cone increased with increasing cone length ($r = 0.33$).

Sound Seeds

Mean number of sound seeds per cone per tree was not significantly different among areas (Table 2) but varied significantly among trees. The percentages of sound seed increased significantly with increasing cone length ($r = 0.20$) but did not change significantly with increasing numbers of cones per cluster when all areas were pooled. Because total seeds per cone did not vary significantly among areas, the nonsignificant variation in sound seeds was expected. The increase in sound seed percentages with cone length and the nonsignificant change associated with increasing numbers of cones per cluster indicates that the percentage of sound seed does not decline even though trees produce larger and multiple cones per cluster. Cone length may thus serve as an indicator of sound seed, providing insect damage is negligible. Assuming insect-caused seed loss is negligible, longer cones should be selected over shorter cones because they have a greater probability of containing more sound seed.

Hollow Seeds

The mean number of hollow seeds per cone varied significantly among areas (Table 2) and

TABLE 3. Frequency of cones by cone length and by cones per cluster, all areas, Arizona 1982–1983.

Cone length (cm)	Frequency (%)	Number cones per cluster	Frequency (%)
<6.0	11	1	11
6.0–9.0	80	2	43
>9.0	9	3	32
		4	11
		5	3

trees within areas. The percentage of hollow seeds decreased significantly with increasing cone length (r = 0.22) but did not change significantly with increasing numbers of cones per cluster when all areas were pooled. The relationships between the number or percentages of hollow seeds and cone length and cones per cluster were the opposite of those for sound seeds.

The greater percentage of hollow seeds associated with shorter cone length suggests that some factor(s) causing poorer cone development might also be associated with greater hollow seed production. Cones that fail to develop to full size also fail to produce a higher percentage of sound seed. Most "hollow" seeds had a small shriveled remnant inside the seedcoat, although a small percentage were completely hollow. Whether these "hollow" seeds resulted from physiological disfunction or insect damage is not certain. Seedbugs were not observed in the areas, so their influence, if any, was minimal.

Megastigmus-infested Seed

Megastigmus-infested seed varied significantly among areas and among trees within areas, which agrees with the results of Schmid et al. (1984). In general, *Megastigmus* (Hymenoptera: Torymidae) levels of damage were less in 1983 than in 1982. In four of five areas common to both studies, mean numbers of *Megastigmus*-infested seed declined significantly in 1983. This indicates the substantial annual fluctuations occurring in the incidence of infestation, caused perhaps by substantial changes in *Megastigmus* population levels.

The percentage of *Megastigmus*-infested seed remained about the same regardless of cone length or numbers of cones per cluster. Thus, *Megastigmus* damage did not have an important influence on the trend in the percentage of sound seed associated with these two variables. Also, the presence of two or more cones in a cluster did not apparently induce females to oviposit more eggs such that the incidence of damage increased with an increasing number of cones per cluster.

Cone Characteristics

Eighty percent of the cones were 6–9 cm in length, with the remaining 20% of the cones about equally present as shorter and longer lengths (Table 3). Two-cone clusters were the most abundant, whereas five-cone clusters were relatively rare.

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NEW SPECIES OF *PROTOCEDROXYLON* FROM THE UPPER JURASSIC OF BRITISH COLUMBIA, CANADA

David A. Medlyn[1] and William D. Tidwell[2]

ABSTRACT.—*Protocedroxylon macgregorii* sp. nov., from Jurassic strata of British Columbia, Canada, is the first reported occurrence of this genus in North America. *Protocedroxylon macgregorii* combines the tracheal pitting of the araucarians with the crossfield pitting of modern genera of the Abietineae. This species is similar to the type species *Protocedroxylon araucarioides*. They differ in that *P. araucarioides* has tangential pitting, tracheid septations, and entirely uniseriate rays. These features are lacking in *P. macgregorii* with the exception of the rays, which are partially biseriate in the latter species. *Protocedroxylon macgregorii* has traumatic resin canals or cysts that have not been reported in *P. araucarioides*.

Protocedroxylon was proposed by Gothan (1910) for woods combining characters of abietineous and araucarian conifers. The type species *Protocedroxylon araucarioides* Gothan (1910) was described from Upper Jurassic strata near Esmarks Glacier of Spitzbergen. Tracheal pitting of *P. araucarioides* is considered araucarioid, whereas its crossfield pitting is typically abietineous. Hence, the generic epithet of the type species refers to its abietineous characters, and the specific epithet implies araucarian affinities.

Specimens of the petrified wood in this report were collected by D. C. McGregor of the Geological Survey of Canada from the northwest shoulder of an unnamed mountain situated about 2.5 km east of Elbow Mountain (across Graveyard Creek). The locality is at about 51°9′ N Latitude and 123°5′ W Longitude. The age is considered Lower Portlandian (Upper Jurassic) based upon the ammonite *Buchia mosquensis*, which occurs at several levels within the unit (Jeletzky and Tipper 1967). The largest specimen of fossil wood measures approximately 15 cm long and 10 cm in diameter and consists of mature secondary xylem only. This specimen falls within the general parameters of *Protocedroxylon* as defined by Gothan (1910). Since it differs from other species of this genus, it is proposed as a new species.

SYSTEMATICS

Coniferales

Protopinaceae

Protocedroxylon Gothan

Protocedroxylon macgregorii sp. nov.

Figs. 1–12

DIAGNOSIS.—Growth rings distinct, 19–70 tracheids wide, transition from early to late wood gradual, occasionally abrupt; late wood tracheids radially flattened with narrow elliptic lumens and walls 5–7 μm thick, early wood tracheids large, angular, with walls 4–7 μm thick, lumens large, 50–85 μm in radial diameter; traumatic resin canals occasionally present having 6–12 thick walled and pitted epithelial cells, horizontal resin canals absent; rays uniseriate, frequently partially biseriate, occasionally entirely biseriate, never multiseriate, 1–40 cells high (commonly 12–25); individual ray cells round to elliptical, largest cells 17–25 μm wide, 25–30 μm high; tracheal pitting variable, 1–4 seriate; early wood tracheal pitting typically multiseriate, alternate and tightly appressed (araucarioid), rarely opposite or in stellate pit clusters; late wood pitting mostly uniseriate, separate or contiguous; pit borders 17–25 μm in diameter with rounded apertures; tangential pits and wood parenchyma absent; rays homogenous, ray parenchyma highly resinous, horizontal and tangential walls pitted, end walls slightly to

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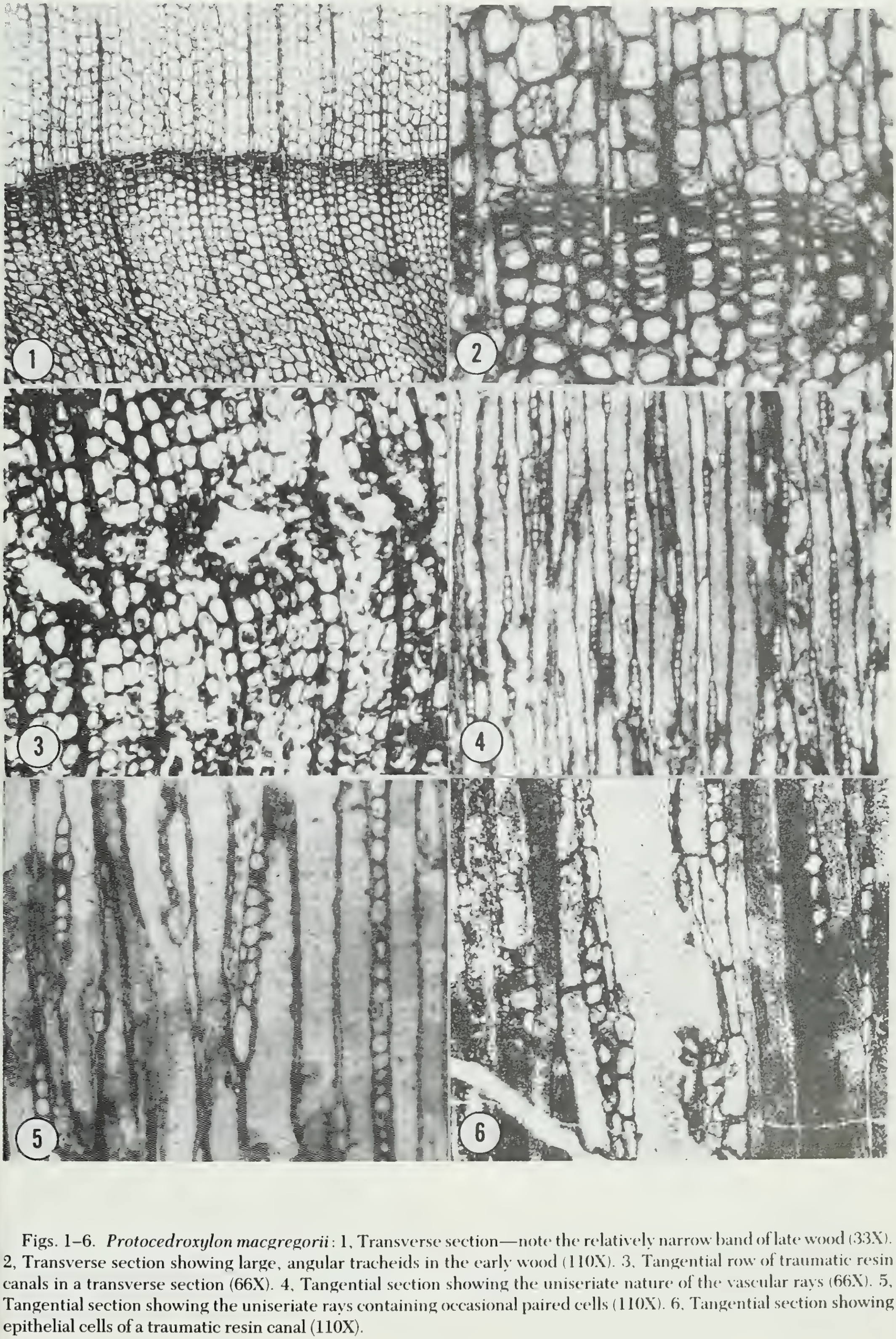
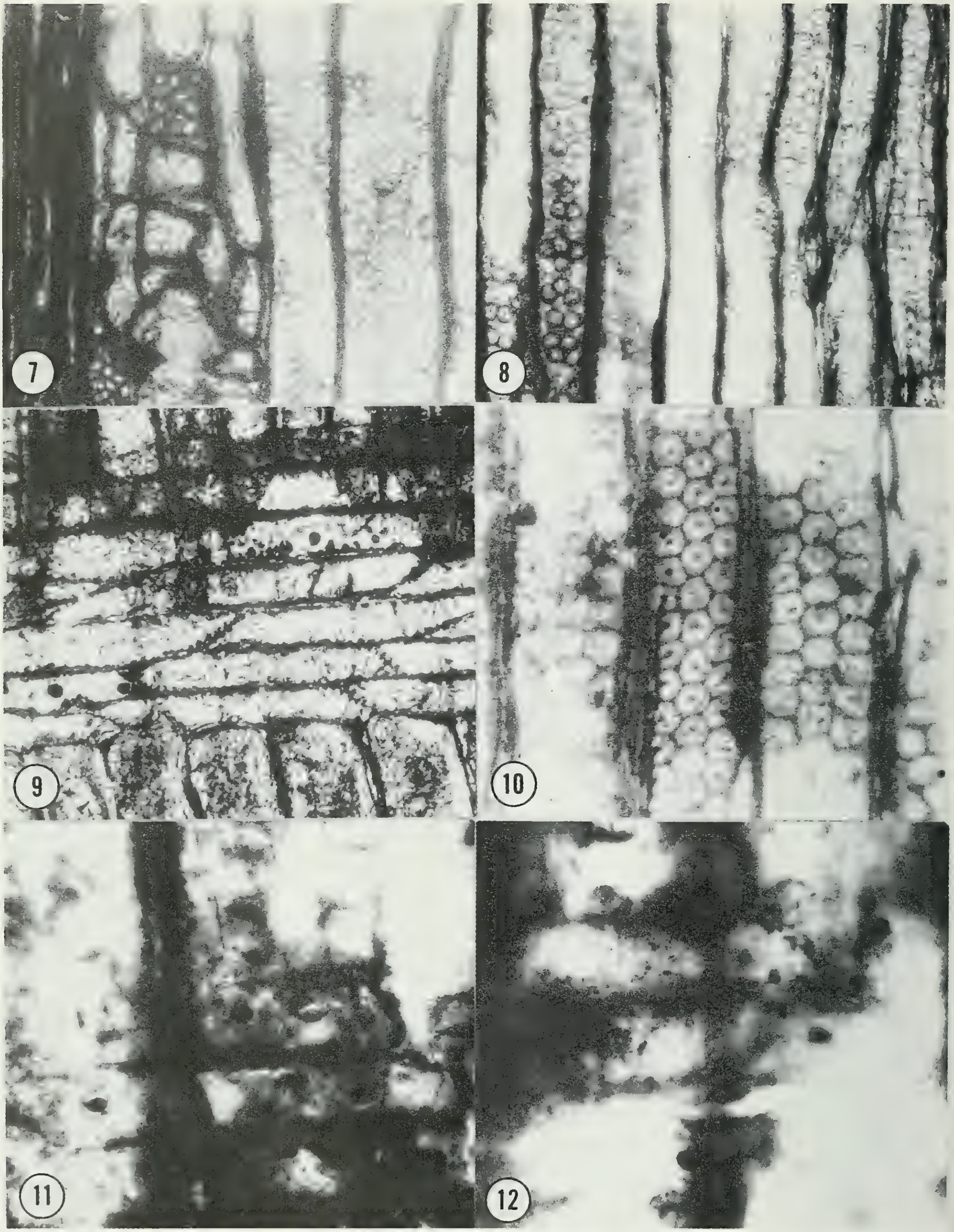


Figs. 1–6. *Protocedroxylon macgregorii*: 1, Transverse section—note the relatively narrow band of late wood (33X). 2, Transverse section showing large, angular tracheids in the early wood (110X). 3, Tangential row of traumatic resin canals in a transverse section (66X). 4, Tangential section showing the uniseriate nature of the vascular rays (66X). 5, Tangential section showing the uniseriate rays containing occasional paired cells (110X). 6, Tangential section showing epithelial cells of a traumatic resin canal (110X).



Figs. 7–12. *Protocedroxylon macgregorii*: 7, Radial view of a traumatic resin canal illustrating the pitted, thick walled epithelial cells (245X). 8, Radial section showing variation in tracheary pitting, note particularly the stellate pit clusters at the left (160X). 9, Radial section showing the pitted nature of the horizontal and vertical walls of the vascular rays (300X). 10, Radial section showing araucarioid tracheal pitting that typifies this genus (300X). 11, Radial section showing crossfield pitting, note the bordered pit (arrow) (750X). 12, Closeup of radial view of vascular ray (150X).

acutely oblique, crossfields with 1–3 circular, thinly bordered pits (7–10 μm), pit borders 2 μm wide, with rounded to elliptic lumens, the cross-field pits tend to be horizontally aligned.

HOLOTYPE: Geological Survey Canada Collection No. 6776.

PARATYPE: Brigham Young University 5027.

ETYMOLOGY: This species is named for its collector D. C. McGregor.

DISCUSSION

Since Gothan (1910) described the genus *Protocedroxylon*, the history of this taxon has become rather complex. *Metacedroxylon* was proposed by Holden (1913) to replace *Protocedroxylon* Gothan on the basis that the latter name implies an abietineous affinity. She further concluded that because *Metacedroxlyon* lacked "bars of Sanio" and possessed araucarioid pitting, it could be none other than an araucarian conifer. In the early 1900s many workers, including Gerry (1910), Holden (1913), and Stopes (1916), debated the diagnostic value of bars or rims of Sanio (crassulae). The presence of crassulae was said to indicate possible abietineous relationships, and the absence of crassulae suggested araucarian affinities. Holden (1913) maintained that presence or absence of crassulae was the only sure criterion for diagnosing fossil conifers. This theory was later investigated by Bailey (1933), who concluded that, although crassulae do not occur in the wood of extant Araucariaceae, it is fallacious to assume that these structures would be preserved under all conditions of fossilization.

Metacedroxylon araucarioides (Gothan) Holden and *M. latiporosum* Holden were described by Holden (1913) from the Upper Jurassic of the Yorkshire Coast of England. Holden (1915) later reported *M. scoticum* from the Jurassic Corallian beds of the Sutherland Coast of Scotland. Seward (1919) subsequently pointed out the invalidity of Holden's name and combined *Metacedroxylon* with *Protocedroxylon*.

Stopes (1916) not only questioned the use of *Metacedroxylon* but also *Protocedroxylon* and *Cedroxylon* Kraus (1872), believing them to be "taxonomic misfits." She further added that it is not justifiable to assume an affinity of fossil genera, whose fructifications are unknown, to living genera. Therefore, to her, Gothan's use of the names *Protocedroxylon* and *Cedroxylon* and Holden's use of *Metacedroxylon* all seemed inappropriate. Stopes (1916) then proposed a new genus, *Planoxylon*, in which the principal characters are similar to Gothan's genus *Protocedroxylon*. She assigned two species to her new genus: *Planoxylon hectori* Stopes from the Cretaceous of New Zealand and *Planoxylon lindleii* (Whitham) Stopes. The latter species was first described by Whitham (1833) as *Peuce lindleii* and, since that time, has been shuffled from genus to genus. Stopes (1916) removed *P. lindleii* from *Araucarioxylon* Kraus, where it was previously classified by Seward (1904). This species has since been placed in *Protopiceoxylon* Gothan by Eckhold (1922), *Protocedroxylon* Gothan by Edwards (1925), *Pinoxylon* Knowlton by Read (1932), *Dadoxylon* Endl. by Shimakura (1936), and *Yorkoxylon* Vogellehner by Vogellehner (1968).

Krausel (1949) placed *Protocedroxylon*, as well as various species of *Metacedroxylon, Paracedroxylon* Sinnott, *Paracupressinoxylon* Holden, and *Thylloxylon* Gothan into synonymy with *Araucariopitys* Jeffrey. Vogellehner (1968) subsequently included *Araucariopitys, Metacedroxylon,* and *Planoxylon* in *Protocedroxylon*. Lemoigne (1970) included *Protocedroxylon araucarioides* Gothan, *Metacedroxylon scoticum* Holden, and *Mesembrioxylon libanoticum* Edwards (1929) in the new genus *Embergerixylon* Lemoigne (1968). However, based upon priority, *Protocedroxylon* should have precedent over *Embergerixylon*.

Shilkina and Khudayberdyyev (1971) followed Krausel (1949) and concluded that *Planoxylon* should be separated from *Protocedroxylon* based upon a difference in their tracheal pitting. Nishida and Nishida (1984) retained *Planoxylon* for fossil conifer woods having typical araucarian pitting and vertical pairs of pits in the crossfield.

COMPARISONS

Protocedroxylon has been reported from strata of Middle Jurassic to upper Lower Cretaceous age (Gothan 1910, Seward 1919, Negri 1914, Vogellehner 1968). *Protocedroxylon araucarioides* has been reported from Mesozoic strata of Svalbard, West Spitzbergen, and Manchuria (Gothan 1910, Walton 1927, Shimakura 1940). Among the characteristics of *Protocedroxylon araucarioides*, Gothan made a special point of noting the absence of normally formed resin canals in this species. Axillary or wood parenchyma is sparse to absent in *P. araucarioides*, and its vascular rays are always uniseriate. The horizontal and tangential walls of the ray parenchyma of *P. araucarioides* are heavily pitted and in each crossfield are 1–3 circular pits. The tracheal pitting in *P. araucarioides* is araucarian. It is characterized by uniseriate to triseriate, large, bordered pits (20–24 μm in diameter) with flattened and contiguous borders. Gothan (1910) did not mention the occurrence of crassulae between the bordered pits in this species, and their presence could not be observed in any of his figures. Numerous tangential pits are present in the late wood tracheids.

Protocedroxylon transiens (Gothan) Shilkina and Khudayberdyyev (= *Cedroxylon transiens* Gothan) is similar to *P. araucarioides*. Terminal parenchyma and stellate pit clusters are the only specific differences between *P. transiens* and *P. araucarioides*. Gothan (1907, 1910) cited two occurrences of the former species, one from the Lower Cretaceous of King Charles Land and the other from the Upper Jurassic or Lower Cretaceous of Spitzbergen.

Protocedroxylon macgregorii sp. nov. from the Upper Jurassic of British Columbia is the first report of this genus from North America. *Protocedroxylon macgregorii* is placed in *Protocedroxylon* Gothan on the basis of a predominance of araucarioid tracheal pitting coupled with pitted horizontal and tangential walls of the rays. A combination of the foregoing characters is unique to this genus and the araucarioid type tracheal pitting excludes *P. macgregorii* from either *Araucariopitys* Jeffrey (1907) or *Cedroxylon* Kraus (1872). The absence of normally formed resin canals precludes the possibility of close affinities to *Protopiceoxylon* Gothan.

Protocedroxylon macgregorii is remarkably similar to *P. araucarioides* but differs from it primarily in the absence of tangential pitting, the presence of traumatic resin canals or cysts, the marked absence of tracheid septations (a feature notably present in Gothan's figured specimen, P1.5, Fig. 4 [1910]), and occurrence of partially biseriate vascular rays in *P. macgregorii*. The rays of *P. araucarioides* are always uniseriate. The tracheal pitting of both *P. transiens* and *P. araucarioides* is similar to that of *P. macgregorii*. However, the presence of stellate pit clusters in *P. macgregorii* makes it more closely allied with *P. transiens*, although differing from the latter by not having terminal parenchyma. *Protocedroxylon macgregorii* differs additionally from both *P. transiens* and *P. araucarioides* in having occasional quadraseriate rows of appressed pits. *Yorkoxylon lindleianum* (Whitham) Volgellehner is very similar to *P. macgregorii*, but the height of the vascular rays (1–12 cells), the presence of wood parenchyma (Holden 1914), and the absence of stellate pit clusters in the former are notable differences. *Protocedroxylon hectori* (Stopes) is similar to our species; however, the presence of terminal parenchyma in *P. hectori* and the height of the vascular rays separate them. *Protocedroxylon scoticum* (Holden) Seward (1919), with its predominance of uniseriate pitting, is distinct from *P. macgregorii*. *Protocedroxylon paronai* Negri, from the Cretaceous of North Africa, is not well preserved and therefore not adequately described. A comparison of *P. macgregorii* with *P. paronai* would be inconclusive.

Protocedroxylon macgregorii is similar to several *Protocedroxylon* species from Japan. This species differs from *P. japonicum* Nishida (1967) from the Cretaceous of Choshi by the latter species having septate tracheids and lower rays (1–4, rarely 6 cells high). *Protocedroxylon okafujii* Nishida and Oishi (1982) from the Triassic of Yamaguchi perfecture can be distinguished from *P. macgregorii* by having abundant wood parenchyma in increments and septate tracheids. Also from the same strata as *P. okafujii* are specimens of *P. mineense* (Ogura) Nishida and Oishi. Originally reported as *Araucarioxylon mineense* Ogura (1960), this species was subsequently placed in *Protocedroxylon* by Nishida and Oishi (1982). They further included *P. triassicum* Yamazaki and Tsunada (1981, Yamazaki et al. 1980) in this species. *Protocedroxylon macgregorii* is separated from *P. mineense* by the tangential pitting and septate tracheids in the latter and the presence of triseriate pitting and stellate pit clusters in the former. *Protocedroxylon yezoense* Nishida and Nishida from the Cretaceous Upper Yezo Group, Hokkaido differs from *P. macgregorii* in that *P. yezoense* has septate tracheids, typically uniseriate pitting, the presence of wood parenchyma, and lower rays (1–28 cells high) that do not occur in *P. macgregorii*.

Protocedroxylon macgregorii and *Protopiceoxylon canadense* Medlyn and Tidwell (1979), are presently the only species of petrified conifer wood of Jurassic age reported from British Columbia. Additional studies of fossil woods, as well as compression materials from this area, will be necessary before the nature and composition of the Jurassic forest of this region can be fully understood.

ACKNOWLEDGMENTS

We express appreciation to Dr. S. R. Ash of the Department of Geology, Weber State College, Ogden, Utah, for reviewing this paper. We also appreciate the critical comments of Dr. E. M. V. Nambudiri, who examined the specimens. Thanks are also due to Dr. Brian Norford of the ISPG, Calgary, Alberta, for sending us the specimens from which *Protocedroxylon macgregorii* was described. Partial financial support for this study is also acknowledged from the Society of Sigma Xi and Brigham Young University Research Grant 115-22-053.

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NEW TAXA AND NOMENCLATURAL CHANGES IN UTAH PENSTEMON (SCROPHULARIACEAE)

Elizabeth C. Neese[1]

ABSTRACT.—New taxa include *Penstemon angustifolius* Pursh var. *dulcis* Neese, *P. leonardii* Rydb. var. *higginsii* Neese, *P. scariosus* Pennel var. *cyanomontanus* Neese, and *P. thompsoniae* (Gray) Rydb. var. *desperatus* Neese. New nomenclatural combinations include: *Penstemon acaulis* L. O. Williams var. *yampaensis* (Penl.) Neese, *P. duchesnensis* (N. Holmgren) Neese, *P. leonardii* Rydb. var. *patricus* (N. Holmgren) Neese, and *P. pachyphyllus* Gray ex Rydb. var. *mucronatus* (N. Holmgren) Neese.

Studies leading to a revision of *Penstemon* for the Utah flora project dictated the following nomenclatural changes and demonstrated the presence of some taxa that require names and descriptions. The justification for these decisions will appear in the version of the Utah flora to be published subsequently.

***Penstemon acaulis* L. O. Williams var. *yampaensis* (Penl.) Neese** stat. nov. [based on *Penstemon yampaensis* Penl. Madroño 14: 156. 1958].

***Penstemon angustifolius* Pursh var. *dulcis* Neese** var. nov. Similis *P. angustifolius* var. *venosus* sed in foliis gracilioribus et colore floribus omnibus roseolioribus differt. TYPE: USA Utah. Millard Co.; T17S, R5W, S35, SE1/4, Canyon Mts.–Sevier Desert, 10 km 200 dgrs from Oak City, 1,586 m, juniper community on aeolian sand, 19 May 1981, S. Goodrich 15403 (Holotype BRY; 7 isotypes distributed previously as *P. angustifolius* Nutt. ex Pursh). ADDITIONAL SPECIMENS: Utah. Millard Co.; T17S, R5W, S36, NW1/4, Canyon Mts., 9 km 195 dgrs from Oak City, S. Goodrich 15402; ibid., T17S, R5W, S36 NW1/4, Canyon Mts., Clay Springs Wash, 9 km 195 dgrs SW of Delta, S. Goodrich 18313; ibid., Millard Sand Dunes, Stanton 5281. Juab Co.; T14S, R5W, Delta, E. Rose 1521; ibid., Little Sahara Dunes, K. H. Thorne 78 (all BRY). Four-wing saltbush, sagebrush-eriogonum, and juniper communities at 1,400 to 1,650 m in Millard and Juab counties; endemic; 9 (0).

***Penstemon duchesnensis* (N. Holmgren) Neese** stat. nov. [based on *Penstemon dolius* var. *duchesnensis* N. Holmgren Brittonia 31: 219. 1979].

***Penstemon leonardii* Rydb. var. *higginsii* Neese** var. nov. Plantis similis *P. leonardii* var. *leonardii* sed in corollis lavandulis (nec caeruleis) et plus suffruticosis differt. TYPE: USA Utah. Washington Co., T39S, R13W, S20, along the Browse road to Guard station, E side of Pine Valley Mts., at 2,000 m, sandy soil, pinyon-juniper-mountain brush community, 7 June 1983, Larry C. Higgins 13578 (Holotype BRY, 4 isotypes distributed previously as *Penstemon*). ADDITIONAL SPECIMENS: Utah. Washington Co., Pine Valley, 26 June 1941, W. P. Cottam 8863; ibid, Kolob, 30 July 1965, A. H. Barnum 1407; ibid., Beaverdam Mts., 18 June 1966, Larry C. Higgins 692; ibid., summit of the Beaverdam Mts., 14 June 1970, Larry C. Higgins 3393; ibid., 21 km S of Enterprise, 18 June 1970, Larry C. Higgins 3483; ibid., 4 km N of Cougar Pass, 17 June 1976, N. D. Atwood 6824; ibid., Pine Valley Mts., 8 June 1981, N. D. Atwood 7886; ibid., Kolob Terrace, 7 July 1981, S. L. Welsh 20696; ibid., 10 km S of Enterprise, 10 June 1983, N. D. Atwood 9355; ibid., Cole Flat on road to Slaughter Creek, 10 June 1983, Larry C. Higgins & N. D. Atwood 13711; ibid., Kolob Plateau, 14 July 1983, B. Albee 5615; ibid., Pine Valley Mts., 18 June 1984, Larry C. Higgins 14392; ibid., Kolob Terrace, 7 June 1984, S. L. Welsh, Larry C. Higgins, and K. Thorne 22926; ibid., Pine Valley mts., 8 July 1984, B. & J. Franklin 843; ibid., 6 km E of Enterprise, 13 June 1985, Larry C. Higgins & E. Higgins 15710; ibid., Pine Valley Mts., 6 July 1985, G. Baird 1705; ibid., N slope of Pine Valley Mts., 26 June 1985, E.

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Neese 17092 (all BRY). Pinyon-juniper, mountain brush, ponderosa pine-manzanita, and aspen conifer communities at 2,000 to 2,750 m in the Valley and Bull Valley mts. and Kolob Plateau, Washington County; endemic; 18 (i). Earlier reports of *P. thurberi* Torr. from Washington County belong here.

***Penstemon leonardii* Rydb. var. *patricus* (N. Holmgren) Neese** [based on: *Penstemon patricus* N. Holmgren Brittonia 31: 238. 1979].

***Penstemon scariosus* Pennell var. *cyanomontanus* Neese** var. nov. Similis *P. scariosus* var. *garrettii* (Pennell) N. Holmgren sed in corollis glandularibus extus caeruleo-purpureis plerumque et caulibus plus decumbentibus differt. TYPE: USA Utah. Uintah Co., T4S, R25E, S25 S/E1/4, near Reservoir, Blue Mountain Plateau, 2,349 m, in dry creek bed, with *Ivesia, Carex*, and *Rumex*, 20 June 1982, E. Neese et al. 11808 (Holotype BRY; five isotypes distributed previously as *Penstemon*). ADDITIONAL SPECIMENS: Utah. Uintah Co., Doug Chew's cabin, Blue Mt., 2 June 1956, S. L. Welsh 470; ibid., Warren Draw, 15 June 1978, E. Neese 5693; ibid., Blue Mt. Plateau, 12 June 1982, E. Neese & B. Neely 11752; ibid., 6 July 1982, F. Smith & J. Trent 1742; ibid., Yampa Plateau, 20 June 1982, F. Smith, E. Neese, & J. Trent 1703; ibid., Blue Mt., 13 June 1982, K. Thorne & B. Neely 2003; ibid., 6 July 1982, E. Neese & K. Snyder 11908; ibid., 9 July 1983, R. Dorn 3881 (all BRY). Colorado. Moffat Co., top of Douglas Mt., 1938, Brown 194 (BRY). Sandstone crevices in sagebrush-grass communities on the Blue Mountain Plateau summit near the Colorado/Utah border, Uintah Co.; Colorado; a Uinta Basin endemic; 13 (vi). The taxon was previously reported from the region as *P. cyanocaulis* Payson (Welsh 470 BRY).

***Penstemon thompsoniae* (Gray) Rydb. var. *desperatus* Neese** var. nov. Ab *P. thompsonae* var. *thompsonae* in caulibus et inflorescentiis longioribus et foliis minoribus differt. TYPE: USA. Utah. Beaver Co., ca 8 mi SW of Sawtooth Peak, Indian Peak Range, T29S, R19W, S3, at 2,013 m, 26 May 1976, S. Welsh, K. Taylor, & F. Peabody 13287 (Holotype BRY; 2 isotypes distributed previously as *P. thompsonae*). ADDITIONAL SPECIMENS: Utah. Beaver Co., Hamblin Valley, 31 May 1978, K. Ostler & D. Anderson 1197; ibid., Wah Wah Mts., 22 June 1978, K. Ostler 1465 (all BRY). Iron Co., Hamblin Valley, 16 June 1978, K. Ostler & D. Anderson 1407; ibid., ca 21 km W of Enterprise, 13 June 1985, L. C. & E. Higgins 15725; ibid., Enterprise-Panaca road, 6 km E of the Nevada border, 12 June 1984, N. H. & P. K. Holmgren 10445 (all BRY). Sagebrush and pinyon-juniper communities at 1,800 to 2,075 m in Beaver and Iron counties; Nevada; 6 (0). One specimen tentatively assigned here (Atwood 5151 BRY) has stems unusually long, and is probably more closely allied to materials from the Mohave Strip region of Arizona. Possibly it represents still another taxon worthy of naming. Other, as yet unrecognized, infraspecific taxa may occur within the species beyond Utah.

***Penstemon pachyphyllus* Gray ex Rydb. var. *mucronatus* (N. Holmgren) Neese** stat. nov. [based on: *Penstemon mucronatus* N. Holmgren Brittonia 31: 234. 1979].

RELICT OCCURRENCE OF THREE "AMERICAN" SCOLYTIDAE (COLEOPTERA) IN ASIA

Stephen L. Wood[1] and Hui-fen Yin[2]

ABSTRACT.—The first non-American representatives of the bark beetle genus *Pseudopityophthorus*, of the subtribe Corthylina (Corthylini), and of the *Ips concinnus* species group are named. All are apparently relicts of an early faunal exchange with North America. The new taxa include: *Gnatharus*, new genus, and its type-species *Gnatharus tibetensis*, new species (Tibet); *Xenophthorus*, new subgenus, and its type-species *Pseudopityophthorus* (*Xenophthorus*) *peregrinus*, new species (Tibet), and *Ips orientalis*, new species (Tibet, China). The intercontinental exchange of other taxa in Scolytidae are also mentioned.

Faunal interchange between North America and Asia has been widely recognized ever since the discovery of America. Among the Scolytidae this has included the invasion of the Eurasian genus *Polygraphus* (about 45 species) into North America (3 species), *Phloeosinus* (40 Asian to 29 American spp.), *Cryphalus* (over 200 Asian to 3 American spp.), *Dryocoetes* (over 80 Asian to 7 American spp.) *Orthotomicus* (12 Asian to 1 American spp.), *Trypodendron* (12 Eurasian to 5 American spp.), etc. Migration in the opposite direction has included *Carphoborus* (21 American to 14 Eurasian spp.), *Scolytus* (over 60 American to 47 Eurasian spp.), *Pityophthorus* (over 300 American to about 35 Eurasian spp.), *Ips* (33 American to 18 Eurasian spp.), *Pityokteines* (6 American to 3 Eurasian spp.), etc. In each case anatomical and phylogenetic diversity in the invaded area is conspicuously less than in the area of origin such that no species group occurred in the invaded area that was not also present in the area of origin. More species groups in each genus always occurred in the area of origin than occurred in the invaded area.

In view of the above, it should be expected that additional examples of faunal exchange will be found. The Eurasian occurrence of *Dendroctonus micans* Kugelann, a geographical replacement species of the subpolar *D. punctatus* LeConte, in a genus that otherwise was exclusively American, has been known for almost a century. However, the discovery of *D. armandi* Tsai & Li in China, with no allied sister species in America was surprising. Equally unexpected was the discovery that the species named from China as *Gretshckinia mongolica* Sokanovskii actually belongs to the American genus *Pseudothysanoes*, and, in fact, is the only represenative of its tribe in Asia.

In a review of the Scolytidae of China, representatives of three additional groups thought to be exclusively American were found. The first is a previously unknown species of *Ips* that is allied to *I. concinnus* (Mannerheim). The second is an aberrant species of *Pseudopityophthorus*. The third is a previously unknown genus in the subtribe Corthylina, the first native species found outside of America. It is anticipated that additional relicts of an early faunal exchange will be found in both Asia and North America as the faunas become more completely known. These new taxa are described as follows.

Ips orientalis, n. sp.

This species is distinguished from the closely allied *concinnus* (Mannerheim) of western North America by the stouter body form, by the absence of a frontal fovea and tubercle, by the less deeply excavated elytral declivity, with the lateral margins less strongly elevated and the denticles smaller, and by the much more pronounced sexual dimorphism of the declivity.

MALE.—Length 4.4 mm (paratypes 3.5–4.4 mm), 2.3 times as long as wide; color dark reddish brown.

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Frons resembling *concinnus* except tubercles distinctly smaller, particulary those on epistomal margin; central fovea entirely absent, median tubercle on epistomal margin and not larger than other tubercles. Antennal club with base significantly thicker and more corneous, sutures equally procurved.

Pronotum as long as wide, essentially as in *concinnus* except discal area much shorter.

Elytra 1.3 times as long as wide, 1.4 times as long as pronotum; basic outline and structure as in *concinnus* except stouter, discal punctures less numerous, larger, deeper, confused; declivity of same basic structure as *concinnus* except much less strongly excavated, rather weakly explanate, lateral margins on upper half rounded, all denticles smaller and more broadly conical, 2 without a ventral carinate ridge extending toward 3. Vestiture about as in *concinnus*.

FEMALE.—Similar to male except frons with a poorly formed central fovea about as in female *concinnus*; elytral declivity with apical margin subacute, but not explanate, and not extending as far laterally; declivital excavation narrower and lateral margins not as high as in male.

TYPE LOCALITY.—Baxoi, Xizang (Tibet).

TYPE MATERIAL.—The male holotype, female allotype, and one male and two female paratypes are from Baxoi, Xizang (Tibet), 18-VIII-1973, *Picea*, Huang Fu-sheng. Two female paratypes are from Riowqe, Xizang (Tibet), 19-VIII-1976, same collector and host. One male and two female paratypes are from Barkam, Sichuan, 24-VII-1955, *Picea*, Qui De-xun. One male paratype appears to be from the type locality, taken 18-VI-1974. The holotype, allotype, and four paratypes are in the Institute of Zoology, Academia Sinica, five paratypes are in the Wood collection.

NOTES.—The discovery of this species is significant because it represents the first occurrence of this distinctive species group in an area outside of North America. Additional significance is found in the fact that it is by far the most primitive member of its group, and of *Ips*, and adds to the evidence that both *Ips* and *Orthotomicus* were derived from *Acanthotomicus*, and that the obliquely truncate antennal club of this tribe is not primitive in this tribe.

Pseudopityophthorus Swaine

The genus *Pseudopityophthorus* has consisted of 23 species from North and Central America and one species from northern South America (Colombia). All bore in the phloem tissues of *Quercus* where they form characteristic transverse biramous parental tunnels. It was most surprising, therefore, to find a species in this uniquely American genus in Asia, also in *Quercus*. While this species is clearly allied to the first six species in my key (Wood, 1982, Great Basin Nat. Mem. 6: 966), it is thought appropriate to place it in a separate subgenus, based primarily on characters of the antennal club.

Xenophthorus, new subgenus.—Antennal club broadly oval, almost subcircular, sutures profoundly procurved, suture 1 attaining middle of club; anterior margin of pronotum not regularly serrate. Other characters as in primitive members of genus as described for the type-species.

Type-species.—*Pseudopityophthorus (Xenophthorus) peregrinus*, described below.

Pseudopityophthorus peregrinus, n. sp.

This species is distinguished from all other members of the genus by the very strongly procurved sutures of the antennal club, by the presence of strial punctures on both disc and declivity, by the long vestiture, and by other characters described below.

FEMALE.—Length 1.9 mm (paratypes 1.7–2.0 mm), 3.0 times as long as wide; color very dark brown.

Frons convex, a moderate transverse impression on lower third; surface reticulate-granulate, upper half and sides with sparse, rather coarse granules; vestiture sparse, rather long, hairlike. Antennal scape shorter than club, slender; funicle 5-segmented; club 1.17 times as long as scape, 1.17 times as long as wide, sutures broadly, very strongly procurved, marked by rows of setae, 1 extending slightly beyond middle of club.

Pronotum resembling *granulatus* Blackman except posterior areas more coarsely punctured and anterior margin unarmed except for about four irregularly placed serrations.

Elytra 1.8 times as long as wide, 1.5 times as long as pronotum; striae not impressed, punctures small; moderately deep, in rows, spaced by about diameter of a puncture; interstriae almost smooth and shining, three times as wide as striae, punctures feebly granulate, half as large as those of striae, uniseriate, as closely spaced as strial punctures. Declivity steep, convex; striae continued to apex, punctures much smaller than on disc; interstriae very slightly shagreened, 1 weakly elevated, all with punctures replaced by small uniseriate granules. Vestiture consisting of short strial hair and long, coarse, pointed interstrial hair; each interstrial seta longer than distance between rows, up to twice as long on declivity.

TYPE LOCALITY.—Zayü, Xizang (Tibet).

TYPE-MATERIAL.—The female holotype and four female paratypes were taken at the type locality on 2-VIII-1973, from *Quercus*, by Huang Fu-sheng.

The holotype and two paratypes are in the Zoological Insititute, Academia Sinica, two paratypes are in the Wood collection.

Gnatharus, n. g.

This genus is the only native member of the subtribe Corthylina to occur outside of America. Although aberrant in all characters, it appears most nearly allied to *Gnathotrupes* Schedl to which it is remotely related at best. The prothoracic precoxal flange resembles that of *Tricolus* Blandford.

DESCRIPTION.—Frons convex in both sexes, without special sculpture or ornamentation. Eye oval, finely faceted, more than one-third divided by an emargination. Antennal scape club-shaped, slightly shorter than club; funicle 4-segmented; club subcircular, with two rather strongly procurved sutures marked by both grooves and rows of setae. Pronotum sexually dimorphic, female much as in small *Gnathotrupes,* summit at middle, anterior slope strongly declivous and armed by numerous small asperities, very finely sculptured on posterior half, male weakly declivous in front, asperities largely obsolete, carinate anterior margin extended cephalad. Elytra simple, striae obsolete, declivity convex, rather steep, but suture divaricate from middle of declivity, elytra truncated before apex. Protibia in female inflated on posterior face and armed by numerous, confused tubercles; in male flattened, apparently unarmed (concealed from view); lateral margin armed almost to base.

TYPE-SPECIES: *Gnatharus tibetensis* Wood & Yin, described below.

Gnatharus tibetensis, n. sp.

This unique species has no near relatives. It is characterzied as follows.

FEMALE.—Length 2.0 mm (allotype 1.7 mm, paratype 2.0 mm), 2.8 times as long as wide; color yellowish brown, with anterior half of pronotum and posterior half of elytra reddish brown.

Frons broadly convex on upper two-thirds, shallowly, transversely impressed, median line from impression to epistomal margin with a weak double-crested carina; surface strongly reticulate, punctures rather coarse, shallow, not close; vestiture of sparse, fine, short, inconspicuous hair. Eye and antenna as described for genus.

Pronotum 1.2 times as long as wide; sides straight and parallel on posterior two-thirds, broadly rounded in front; anterior margin broadly, almost weakly subcostate, serrations ranging from definite to indefinite, numerous; summit anterior to middle, anterior slope strongly declivous, armed by numerous rather small asperities; posterior areas strongly reticulate, punctures very fine, shallow. Vestiture of fine, short, rather sparse hair; anterolateral angles with a small tuft of longer hair as in some female *Gnathotrupes*. Procoxae contiguous, precoxal piece a simple, transverse partition bent (flanged) cephaled as in most *Tricolus*.

Elytra 1.7 times as long as wide, 1.3 times as long as pronotum; scutellum large, flat; sides almost straight and parallel on more than anterior two-thirds, rather broadly rounded behind except divaricate at suture and with a sublateral denticle; disc smooth shining, striae obsolete, punctures strongly confused, small, distinct, rather close. Declivity rather steep, convex, apex complex; sculpture as on disc; suture beginning to divaricate at middle of declivity, separation gradual and modest to lower fourth, then abruptly (almsot 90 degrees) diverging and curving to meet costal margin in a subspinose point, distance between points equal to almost half of total elytral width. Vestiture of fine, short, rather abundant recumbent hair.

Tibiae wider than normal for tribe, meso- and metatibiae each armed by three socketed teeth, protibiae as described for genus.

MALE.—Similar to female except frontal carina with single summit; pronotum with strongly formed, slightly produced anterior costa (serrations almost obsolete), anterior slope much more gradual, asperities greatly reduced in size, without special tufts of hair on anterolateral angles; posterior face of protibia flat and unarmed.

TYPE-LOCALITY.—Mêdog, Xizang. (Tibet).

TYPE-MATERIAL.—The female holotype, male allotype, and one female paratype were taken at the type locality on 8-IX-1974, 1400 m, from a *Castenopsis* by Huang Fu-sheng.

The holotype and allotype are in the Zoolgocial Institute, Academia Sinica, the paratype is in the Wood collection.

NEW GENUS OF SCOLYTIDAE (COLEOPTERA) FROM ASIA

Stephen L. Wood[1] and Fu-sheng Huang[2]

ABSTRACT.—*Pseudoxylechinus*, new genus, and *uniformis* (type-species) (Yunnan), *variegatus* (Sanxi), *sinensis* (Yunnan), *rugatus* (Yunnan), and *tibetensis* (Tibet), new species, are described. *Kissophagus tiliae* Niisima, 1910, is also transferred to this genus.

In a review of the Scolytidae of China, a genus new to science was found that appears to be a geographical replacement of the closely related North American *Pseudohylesinus* Swaine. Of the seven species examined, all are substantially smaller than are the species of *Pseudohylesinus* and all breed in angiosperm hosts. The species *Kissophagus tiliae* Niisima (1910, Sapporo Nat. Hist. Soc. 3:2), from Japan, is here transferred to *Pseudoxylechinus*.

Pseudoxylechinus, n. g.

DIAGNOSIS.—This genus is distinguished from *Pseudohylesinus* Swaine by the smaller, closer strial punctures, by the unarmed discal interstriae (except in *rugatus*), by the closer, coarser erect discal interstrial setae, by the more slender, apically pointed interstrial ground setae, by the more strongly flattened antennal club with its apex more broadly rounded, and by their occurrence in angiosperm hosts.

DESCRIPTION.—Allied to *Pseudohylesinus* except species mostly smaller, variegated scale patterns less pronounced to absent. Frons sexually dimorphic, more nearly flattened, often with a median carina or groove. Antennal funicle 7-segmented; club flattened, its apex rather broadly rounded. Elytral striae rather narrow, punctures close; interstriae twice as wide as striae usually unarmed on disc. Interstrial ground setae rather slender, each with its apex pointed.

TYPE-SPECIES: *Pseudoxylechinus uniformis* Wood & Huang.

Pseudoxylechinus uniformis, n. sp.

This species is distinguished from other members of the genus by the large size and by the presence of a median carina on the frons in both sexes.

MALE.—Length 2.6 mm (paratypes 2.5–2.8 mm), 2.2 times as long as wide; color dark brown, vestiture uniformly pale.

Frons convex except moderately impressed on lower two-thirds on median third, impressed area with a fine, long, median carina; surface shining, rather coarsely rugose-punctate laterally and above, smooth, shining, and impunctate near carina; vestiture of rather short, coarse, moderately abundant hair. Eye oval, entire, finely granulate, 3.0 times as long as wide.

Pronotum 0.81 times as long as wide; widest at base, strongly, arcuately converging on basal three-fourths to moderate constriction just behind rather broadly rounded anterior margin; surface smooth, shining, with abundant, minute punctures interspersed with less abundant larger punctures (twice diameter of smaller ones), larger punctures spaced by one to two diameters of a large puncture; small punctures bearing scalelike ground setae, each four times as long as wide, strongly tapered from base to acute point; large punctures each bearing a coarse, slender bristle, each about twice as long as scales.

Elytra 1.5 times as long as wide, 2.1 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather narrowly, unevenly rounded behind; striae weakly impressed, punctures small, deep, close; interstriae twice as wide as striae, small punctures minute, shallow, obscure, central row of bristle-bearing punctures modestly granulate. Declivity moderately steep, convex; interstriae 1 and 3 moderately convex, 2 impressed and narrower than 1 or 3 and without bristles or granules, otherwise sculpture as on disc. Vestiture of rather numerous ground scales, each slightly longer than wide and tapered from its base to acute point; each interstriae with a row of uniseriate, stout bristles, each about three-fourths as long as distance between rows.

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FEMALE.—Similar to male except frons more uniformly convex.

TYPE-LOCALITY.—Nanjiang, Sichuan, China.

TYPE-MATERIAL.—The male holotype, female allotype, and a male and three female paratypes were taken at the type locality on 15-VIII-1958, from a broad leaf tree by Song Shi-mei. One female paratype is from Taibai, Shaanxi, China, V-1981, *Pinus tabulaeformis* (accidental?), by Yang Xu-hui.

The holotype, allotype, and two paratypes are in the Institute of Zoology, Academia Sinica, three paratypes are in the Wood collection.

Pseudoxylechinus variegatus, n. sp.

This species is distinguished from *uniformis* Wood & Huang by the smaller size, by the more broadly impressed, grooved, male frons, by the more uniformly punctured pronotum, and by the very different elytra as described below.

MALE.—Frons 2.0 mm (paratypes 1.8–2.1 mm), 2.1 times as long as wide; color dark brown, vestiture 50 to 70 percent pale, remainder darker.

Frons almost flat on slightly more than lower half, upper half of flattened area with a median impression (groove); surface almost smooth, shining on lower half, with fine, shallow punctures; upper areas rugose-reticulate, with obscure, rugose punctures; vestiture of short, rather stout, moderately abundant setae.

Pronotum resembling *uniformis* except sides on basal half subparallel, more strongly arcuate; surface rather coarsely, deeply, uniformly punctured; vestiture of short, stout, moderately abundant bristles, obscurely bicolored.

Elytra about as in *uniformis* except interstrial tubercles higher, sharper; declivity steeper, uniformly convex, interstriae 2 equal in height and convexity to 1 and 3; interstrial ground setae longer, each about four times as long as wide, each tapered from its base, sharply pointed, bicolored, forming an irregular pattern of pale and darker scales, pale predominate; erect bristles about 1.5 times as long as ground setae, of equal width.

FEMALE.—Similar to male except lower frons more convex, median groove present.

TYPE LOCALITY.—Jiangxian, Shanxi, China.

TYPE MATERIAL.—The male holotype, female allotype, and three male and three female paratypes were taken at the type locality on 5-VIII-1972, from *Elaeagnus* sp., by Huang Fusheng.

The holotype, allotype, and two paratypes are in the Zoological Institute, Academia Sinica, and four paratypes are in the Wood collection.

Pseudoxylechinus tibetensis, n. sp.

This species is distinguished from *variegatus* Wood & Huang by the stouter body form, by the less extensively flattened lower frons and shorter groove, and by the larger interstrial tubercles.

FEMALE.—Length 2.2 mm (allotype 2.1 mm), 2.1 times as long as wide; color very dark brown, vestiture forming a variegated pattern of half pale and half dark scales.

Frons irregularly convex, median groove very short; surface rugose-reticulate, obscurely, rather coarsely punctured; vestiture rather short, coarse, moderately abundant.

Pronotum about as in *uniformis*, surface sculpturing similar to *variegatus* except punctures slightly smaller, setae shorter; slender and stout setae clearly discernable.

Elytra about as in *variegatus* except interstrial tubercles on disc distinctly larger, declivital interstriae 1 distinctly higher than 2 or 3, interstrial ground scales shorter, stouter, each less than twice as long as wide, erect interstrial setae more slender. Vestiture about equally divided between pale and dark.

MALE.—Similar to female except frons less extensively flattened on lower half, median groove much shorter than male *variegatus*. Declivity of allotype destroyed (apparently by a predator).

TYPE LOCALITY.—Zayü, Xizang (Tibet).

TYPE MATERIAL.—The female holotype and damaged male allotype were taken at the type locality on 18-IV-1973, 2500 m, from an unidentified host, by Huang Fu-sheng.

The holotype and allotype are in the Zoological Institute, Academia Sinica.

Pseudoxylechinus sinensis, n. sp.

This species is distinguished from *tibetensis* Wood & Huang by the absence of a frontal groove, by the more slender pronotal and elytral ground setae, and by the (apparently) uniformly pale elytral vestiture.

FEMALE.—Length 1.8 mm (paratype 1.9 mm), 2.0 times as long as wide; color dark brown, vestiture apparently uniformly pale (covered by an incrustation).

Frons convex, distinctly inflated just above epistoma, groove absent; surface obscurely subreticulate and rugose-punctate above, more finely sculptured on lower third; vestiture rather fine, short, inconspicuous.

Pronotum about as in *tibetensis* except scale-like setae much more slender. Elytra as in *tibetensis* except interstrial tubercles smaller, declivity more broadly convex with interstriae 1–3 more equally, uniformly convex, scales in ground vestiture much more slender (each about four times as long as wide) but not longer, apparently of uniform color.

TYPE LOCALITY.—Lijiang, Yunnan, China.

TYPE MATERIAL.—The female holotype and one female paratype were taken at the type locality on 2-IX-1962, from an unidentified host by Song Shi-mei.

The holotype is in the Zoological Institute, Academia Sinica, the paratype is in the Wood collection.

Pseudoxylechinus rugatus, n. sp.

This species is distinguished from other members of the genus by the strongly impressed striae, by the large strial punctures, by the coarse interstrial tubercles, and by the very slender interstrial ground setae.

MALE.—Length 2.2 mm (allotype 2.1 mm), 2.0 times as long as wide; color dark brown, vestiture pale.

Frons shallowly concave from epistoma to upper level of eyes from eye to eye; surface largely obscured by an incrustation but apparently with a short median groove, rugose-reticulate, obscure punctures finely rugose.

Pronotum outline about as in *variegatus*, surface shining, punctures coarse, deep, very close, of mixed sizes; vestiture of recumbent, slender, almost hairlike ground setae and erect, rather stout bristles of almost equal length.

Elytra 1.4 times as long as wide, 1.1 times as long as pronotum; sides almost straight and parallel on basal two-thirds, broadly rounded behind; striae rather strongly impressed, punctures coarse, deep, close; interstriae as wide as striae, each armed by a uniseriate row of closely set, coarse, almost subvulcanate, setiferous tubercles, each tubercle almost as high as wide and almost as wide as interstriae. Declivity steep, convex; punctures and tubercles distinctly smaller than on disc. Vestiture limited to a row of ground setae on each side of each interstriae, each seta slender (about eight times as long as wide), and erect bristles, one arising from each tubercle, each bristle only slightly longer and stouter than ground setae.

FEMALE.—Similar to male except frons convex, modestly inflated just above flattened epistomal area.

TYPE LOCALITY.—Xishuangbanna, Yunnan, China.

TYPE MATERIAL.—The male holotype and female allotype were taken 7-V-1962, 750 m, from *Cassia* sp., by Song Shi-mei.

The holotype and allotype are in the Zoological Institute, Academia Sinica.

NEW *PSEUDOXYLECHINUS* (COLEOPTERA: SCOLYTIDAE) FROM INDIA

Stephen L. Wood[1]

ABSTRACT.—*Pseudoxylechinus indicus* is decribed as new to science from India.

In my review of the Scolytidae of India and China, the genus *Pseudoxylechinus* was discovered and named. A species new to India is here added to the Chinese and Japanese species now in this genus.

Pseudoxylechinus indicus, n. sp.

This species is distinguished from other members of the genus by the strongly, broadly excavated male frons, by the shallowly concave female frons, and by the almost hairlike ground setae on the pronotum and elytra.

MALE.—Length 2.7 mm (allotype 2.4, paratype 2.8 mm), 2.1 times as long as wide; color very dark brown, elytra lighter brown, vestiture pale.

Frons very deeply, broadly concave from epistoma to well above upper level of eyes, from eye to eye, margin from epistoma to eye strongly, acutely carinate; surface rugose-reticulate, punctures sparse, minutely granulate; vestiture sparse, hairlike, rather short except much longer at inner margin of eye.

Pronotum 0.94 times as long as wide, outline as in *variegatus* Wood & Huang; surface shining, coarsely, rather shallowly, rugosely punctured, a few small tubercles in median area near anterior margin; vestiture of moderately abundant, rather long, coarse hair.

Elytra 1.6 times as long as wide, 2.2 times as long as pronotum; outline as in *uniformis* Wood & Huang; striae slightly impressed, puctures small, deep, close; interstriae twice as wide as striae, smooth, shining, punctures sparse, minute, each with a uniseriate row of small tubercles. Declivity rather steep, convex, sculpture as on disc. Vestiture of moderately abundant, short, slender, almost hairlike ground setae, and interstrial rows of erect, equally slender bristles, each bristle slightly more than twice as long as ground setae.

FEMALE.—Similar to male except frons shallowly concave on lower third, modestly convex above, lateral margins on lower third acutely carinate; vertex with a short, median, subcarinate callus.

TYPE LOCALITY.—Rangirum, Darjeeling, Bengal, India.

TYPE MATERAL.—The male holotype, female allotype, and one male paratype were taken at the type-locality on 6-IX-1929, from *Quercus lamellosa*, by J.C.M. Gardner.

The holotype and allotype are in the Forest Research Institute, Dehra Dun, the paratype is in my collection.

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WILDLIFE DISTRIBUTION AND ABUNDANCE ON THE UTAH OIL SHALE TRACTS 1975-1984[1]

C. Val Grant[2]

ABSTRACT.—Distribution and abundance of 215 amphibians, reptiles, birds, and mammals were monitored for 10 years on Utah's Oil Shale Tracts using line transects, mist netting, and live trapping. Wildlife monitoring was conducted in four major vegetation types and during all seasons to establish a quantitative baseline for use in impact identification during oil shale mining. Habitat preferences were established for many species in cold desert vegetation of two types of desert shrub, and juniper and riparian woodlands. Seasonal, annual, and habitat distribution of each class demonstrated a variety of adaptive responses to environmental variables. The most important environmental variables, that is, those factors resulting in a predictable change in wildlife populations, were, in descending order: weather, food resource, shelter, and competition.

Distributional accounts of wildlife are usually limited to a particular class, for instance, birds (Behle and Perry 1975, Hayward et al. 1976, Behle 1981, Cook 1984) and mammals (Durrant 1952, Ranck 1961). Western amphibians and reptiles are treated on a regional basis (Stebbins 1966). Nevertheless, regional accounts of wildlife are available for the Utah portion of the Upper Colorado River Basin (Hayward et al. 1958) or for the Uinta Basin Oil Shale Area (Olsen 1973).

These distributional accounts of wildlife relegate abundance to a subjective reference, such as common, uncommon, rare, occasional, etc. Although Behle and Perry (1975) attempt to quantify abundance, there is a basic flaw in an estimator that rates abundance of the golden eagle (*Aquila chrysaetos*) and the horned lark (*Eremophilia alpestris*) as common (Twomey 1942, Olsen 1973, Behle and Perry 1975, Hayward et al. 1976, Behle 1981). Counting two eagles and 2,000 larks on the same day leaves some question as to what *common* really means.

Temporal accounts of wildlife, that is, residency status, characterize a state (Durrant 1952, Behle and Perry 1975, Hayward et al. 1976), a region (Twomey 1942, Behle 1981), a county (Cook 1984), or an area within a county (Ranck 1961, Olsen 1973). Due in part to the geology of Utah, wildlife that are permanent residents in the southern deserts and high plateaus are transients in the northern basins and mountains. Wildlife that summer in the mountains usually winter in the basins. In other words, as scope changes, residency status changes; yet most accounts defer one to another, regardless of reality.

Spatial accounts of wildlife, that is, distributions by habitat or vegetation type, are essentially absent for most reptiles and broadly stated for most birds (Behle 1981, Walters and Sorenson 1983) and some mammals (Durrant 1952, Hasenyager 1980). Specificity is usually limited to game birds and mammals, some rodents, raptors, and threatened and endangered species.

In an effort to fill some voids, a detailed monitoring program for amphibians, reptiles, birds, and mammals began in 1975 and ended, in part, in 1984 at the Oil Shale Tracts Ua-Ub in the Uinta Basin of northeastern Utah. A species-by-species account is reported herein as well as population dynamics of each wildlife class, except that the mammals are divided into bats, rodents, rabbits, carnivores, and ungulates. A detailed account of birds by feeding guild is presented elsewhere (Steele et al. 1987), as is waterfowl (Steele and Vander Wall 1985) and sampling effort (Steele et al. 1984).

STUDY AREA

Ua-Ub includes 42 km^2 (16 mi^2) of cold desert. Elevation ranged from 1,463 m in the

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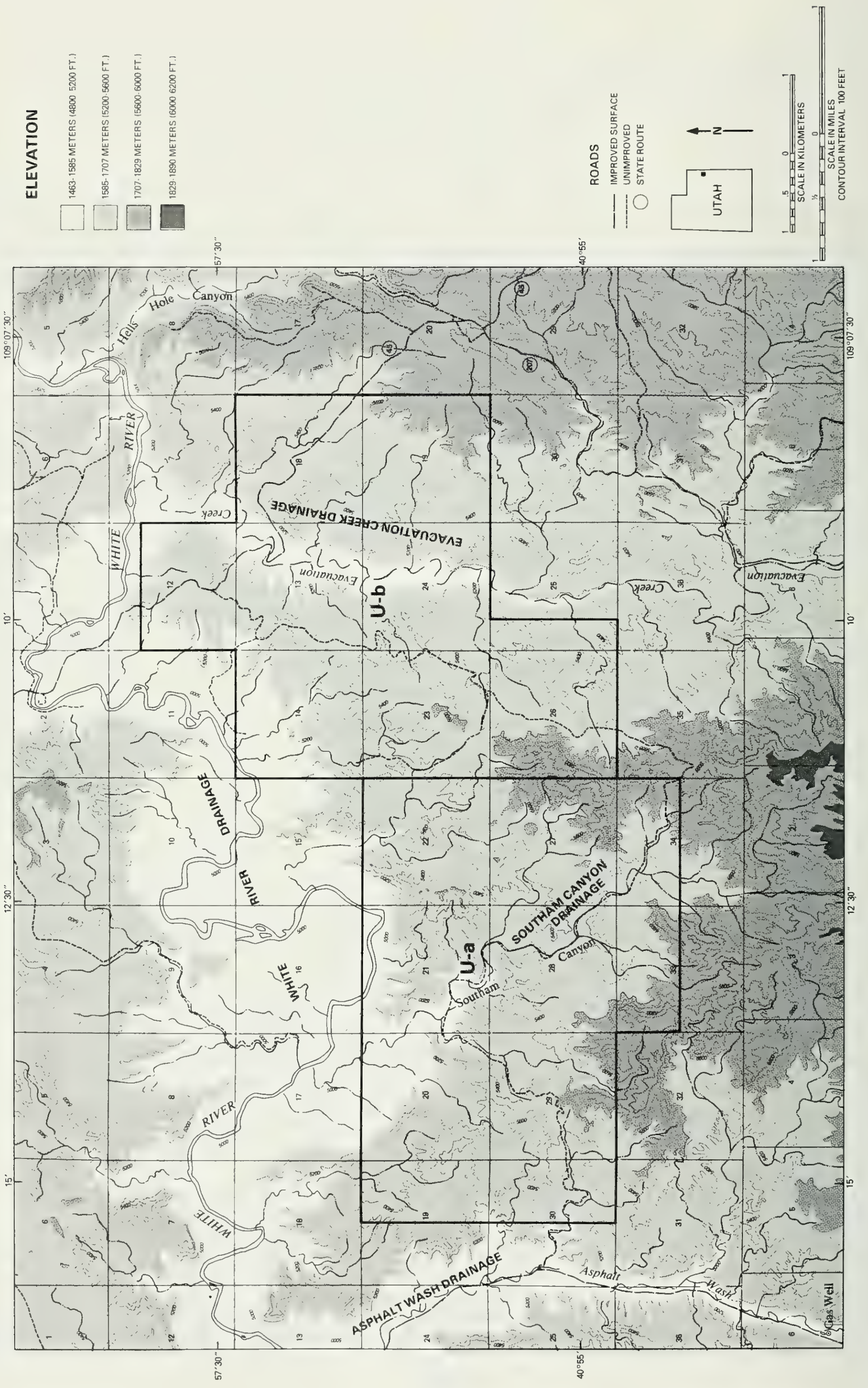
[1] This research was funded by White River Shale Oil Corporation, Salt Lake City and Vernal, Utah.

[2] Bio-Resources, Inc., 135 East Center Street, Logan, UT 84321.


ELEVATION
1463-1585 METERS (4800-5200 FT.)
1585-1707 METERS (5200-5600 FT.)
1707-1829 METERS (5600-6000 FT.)
1829-1890 METERS (6000-6200 FT.)
ROADS
IMPROVED SURFACE
UNIMPROVED
STATE ROUTE
N
UTAH
SCALE IN KILOMETERS
SCALE IN MILES
CONTOUR INTERVAL 100 FEET
109°07'30"
10'
12'30"
15'
57'30"
40°55'
Hells Hole Canyon
WHITE RIVER
WHITE RIVER DRAINAGE
WHITE RIVER
EVACUATION CREEK DRAINAGE
Evacuation Creek
U-b
U-a
SOUTHAM CANYON DRAINAGE
Southam Canyon
ASPHALT WASH DRAINAGE
Asphalt Wash
Gas Well
45
207

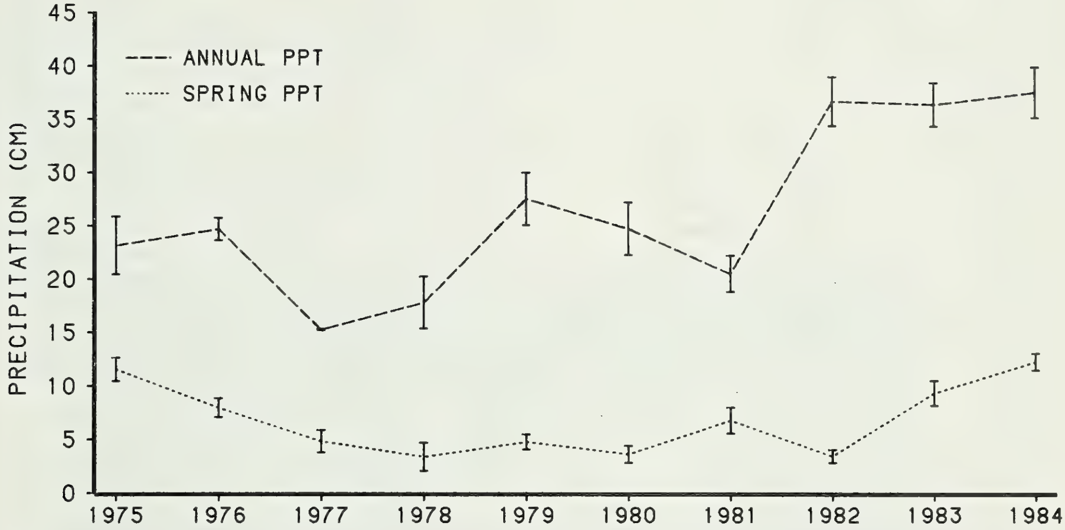


Fig. 2. Annual precipitation (October–September) and spring precipitation (April–June) at Oil Shale Tracts Ua-Ub, Uintah County, Utah (after VTN, Inc.).

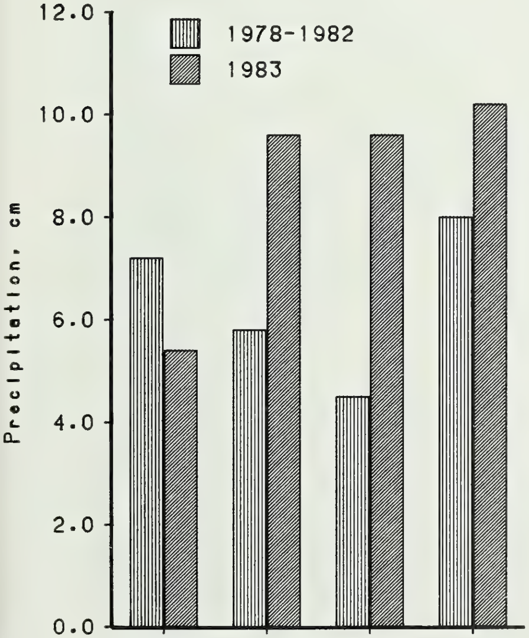


Fig. 3. Seasonal precipitation for 1978–1982 and 1983 at Oil Shale Tracts Ua-Ub, Uintah County, Utah (after VTN, Inc.).

White River fluvium to 1,890 m atop steep walls of Uinta sandstone near the tract's southern perimeter (Fig. 1). Precipitation changed dramatically over the 10 years (Fig. 2); however, seasonal distribution remained the same (Fig. 3). Ambient temperature averaged 8 C and was coldest during the winter along the White River (Fig. 4). Wind speed peaked during the spring, and airflow during the daytime was generally westerly; during the night cold air drained into the White River canyon.

Four vegetation types covered Ua-Ub (Fig. 5). Dominant species in Greasewood vegetation were big sagebrush (*Artemisia tridentata*), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus nauseosus*), and cheat grass (*Bromus tectorum*). Dominant species in Shadscale vegetation were shadscale (*Atriplex confertifolia*), big sagebrush, snakeweed (*Xanthocephalum sarothrae*), and cheat grass. Juniper vegetation was dominated by Utah juniper (*Juniperus osteosperma*), black sagebrush (*Artemisia nova*) in the draws, and cheat grass. Riparian vegetation was dominated by Fremont cottonwood (*Populus fremontii*), tamarisk (*Tamarix tetrandra*), rabbitbrush, greasewood, and cheat grass. Stem leader growth of big sagebursh and biomass of annual and perennial grasses and forbs were used to estimate floral productivity over 10 years (Fig. 6).

MATERIALS AND METHODS

Sampling locations for terrestrial wildlife were within and near Ua-Ub's boundary (Fig.

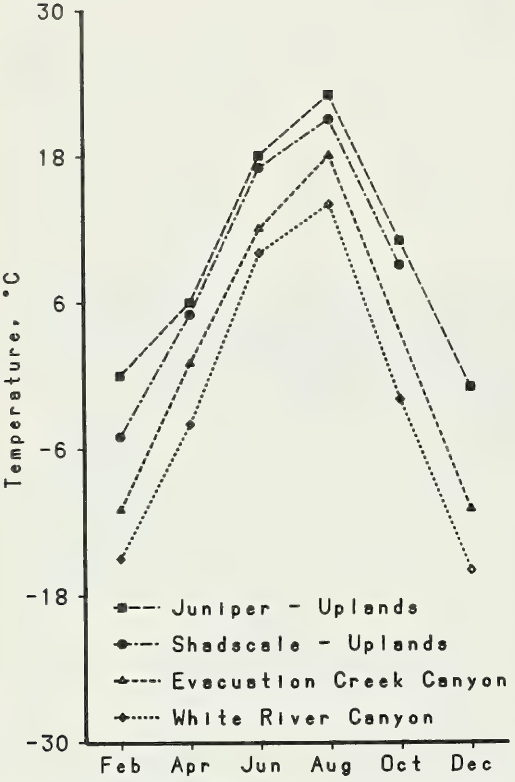


Fig. 4. Seasonal temperature patterns from upland and canyon locations at Oil Shale Tracts Ua-Ub, Uintah County, Utah (after Aerovironment, Inc.).

7), including a mist-netting site for bats at a gas well in the southwest corner of the area mapped. Each vegetation type was sampled for amphibians, reptiles, birds, and terrestrial mammals (including rodents, rabbits, carnivores, and ungulates) by 1 km (0.6 mi) line transects (Emlen 1971). Transects were walked in the early morning for birds, from midmorning to midday for reptiles, and late afternoon to early evening for mammals. All animals observed were recorded by species and number of individuals seen. Perpendicular distance from the transect was estimated for all visual sightings. Auditory identifications were used for species count only, as were tracks, scat, or sign encountered on transect. Transects were surveyed for five consecutive days each month during February, April, June, August, and October. From 1982 to 1984 transects for birds and reptiles were surveyed only during June and for mammals only during August.

For small nocturnal rodents, four large grids (12 x 12 array of Serman live traps) covering 2.73 ha (6.6 acres) were trapped every August in each vegetation type. All traps were baited with oats or barley. All rodents were identified to species, weighed to the nearest gram by 100 g and 500 g capacity Pesola scales, aged (juvenile or adult), sexed, marked for individual recognition, trap site recorded, and released. Seasonal trapping was conducted from 1975 to 1981, with live traps set along transects during February, April, June, August, and October, using the same procedures but fewer traps in different arrays (Steele et al. 1984).

Bats were mist-netted at a small pond formed by low-quality water from an abandoned, artesian natural gas well. Cattails (*Typha* sp.) surrounded the pond in a greasewood–cheat grass–covered section of Asphalt Wash. Nets were checked at 15 minute intervals maximum from sunset to 0400 hr in June and August 1977–1980. Besides recording time of capture, all bats were identified to species; weighed to the nearest gram; forearm, ear, body (nose to base of tail), wing length, and wing width measured to the nearest millimeter; sexed; marked for recapture recognition; and released.

Abundance was expressed as number per kilometer (no/km) for animals sampled on transects. Abundance of rodents captured in the 12 x 12 grids was calculated by dividing the actual area covered by the grid into the number of individuals captured in five nights of trapping and expressed as individuals per hectare (ind/ha). Rodent abundance from seasonal trapping was expressed as individuals per 100 trap nights (ind/100 TN). Bat abundance was expressed as individuals per trap night (ind/TN). Species richness was the number of species that occurred on a transect, in a trap grid, or were mist-netted during a sampling period. Species diversity expressed as H′ after Shannon and Weaver (1964) was calculated from data for a sampling period. Habitat preference and annual changes in abundance, species richness, and species diversity from 1975 to 1984 were tested by two-way analysis of variance (ANOVA) with means ranked by least significant differences (LSD) test (Steel and Torrie 1960). Seasonal preference from 1975 to 1981 was tested by one-way ANOVA and LSD.

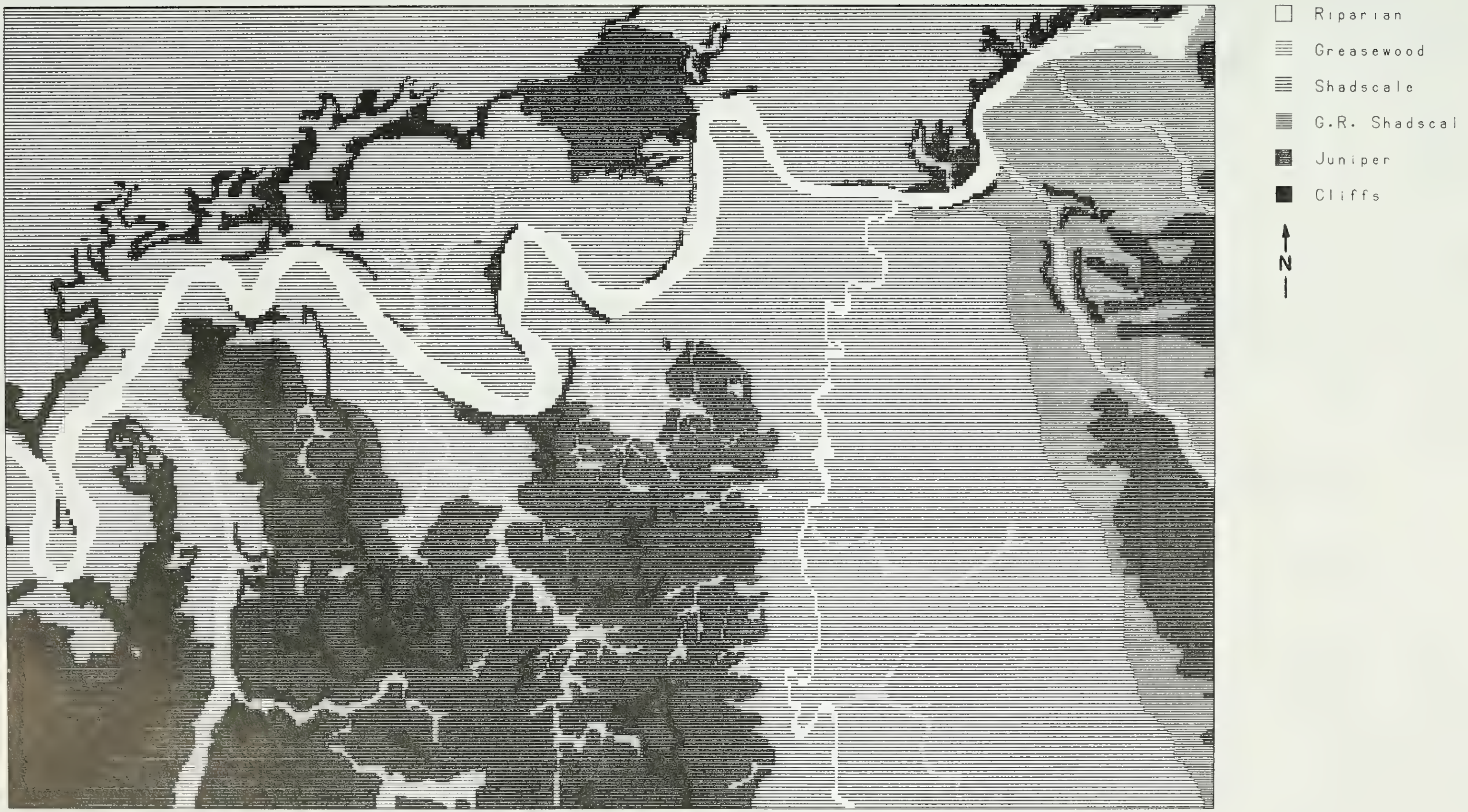

Riparian
Greasewood
Shadscale
G.R. Shadscal
Juniper
Cliffs
N

Fig. 5. Distribution of four vegetation types at Oil Shale Tracts Ua-Ub and surrounding area, Uintah County, Utah. Green River (G.R.) shadscale is subset of shadscale vegetation.

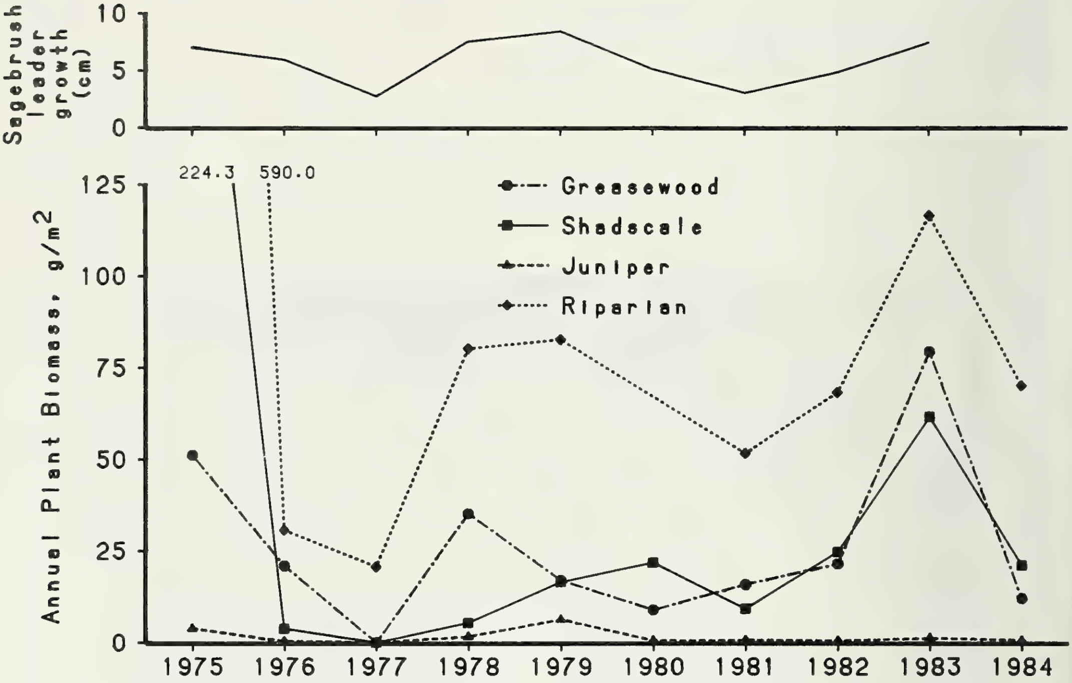


Fig. 6. Sagebrush stem leader growth and annual plant biomass at Oil Shale Tracts Ua-Ub, Uintah County, Utah (after NPI, Inc.).

Species identification of amphibians and reptiles as well as nomenclature was done according to Stebbins (1966), also using Smith (1946) for the latter group of vertebrates. Avian identification was based on Peterson (1961), Robbins et al. (1966), and Behle and Perry (1975) and nomenclature followed AOU (1983). Mammalian identification was based on Ranck (1961), Barbour and Davis (1969), and, primarily, Armstrong (1972), whose nomenclature was also followed. An explanation of abbreviations used in tables and graphs are presented in Table 1.

RESULTS AND DISCUSSION

The number of species of amphibians and reptiles found at Ua-Ub did not differ markedly from the species previously recorded in the Uinta Basin (Table 2). The number of avian and mammalian species, however, was considerably lower at Ua-Ub than in the Basin. This was due to the lack of aquatic as well as higher elevation habitats that support a diversity of birds and mammals absent in the desert portion of the Basin.

Amphibia

SALIENTIA.—Five amphibians occurred at Ua-Ub (Table 3), including a new record, a red-spotted toad (*Bufo punctatus*), found at a small pond in Asphalt Wash, June 1980. The other two toads were the most consistent amphibians, occurring at stock ponds more frequently than along the White River. The two frogs, confined to the White River drainage, were absent more often than not. The tiger salamander (*Ambystoma tigrinum*) included in the Oil Shale Area by Olsen (1973) was not found at Ua-Ub.

Reptilia

SQUAMATA.—Eleven reptiles occurred at Ua-Ub (Table 4). The tree lizard (*Urosaurus ornatus*) was a new record for the Basin. Two other species, the milk snake (*Lampropeltis triangulum*) and night snake (*Hypsiglena torguata*), did not occur at Ua-Ub; however, a milk snake was found and photographed north of Bonanza, Utah, at a small stock pond east of Utah Highway 44 by T. Schultz (WRSP 1977, Final Environmental Baseline Report, SLC, Utah), augmenting Tanner (1957).

TABLE 1. Definition of abbreviations used in text, tables, and graphs for residency status, month, vegetation (habitat) types, and presence/absence.

RESIDENCY STATUS

P = permanent resident: breeding documented, present year-round
p = permanent resident: breeding not documented, present year-round
S = summer resident: breeding documented, present during breeding season, that is, April–October
s = summer resident: breeding not documented
w = winter resident: present October–April
m = migrant: present during spring (April) and/or fall (October)
t = transient: present for short duration and permanent or summer resident at other locales in the Uinta Basin
a = accidental: present infrequently, outside of normal range
? = unknown: present frequently or infrequently for long or short durations at specific or random intervals

VEGETATION TYPES

G = Sagebrush-greasewood
S = Shadscale-sagebrush
J = Juniper woodland
R = Riparian woodland
Subscript p = pond/marsh

PRESENCE/ABSENCE

* Present: Species observed, captured, heard, or identified by sign at one or more times during one year
– Absent: Species not observed, captured, heard, or identified by sign at one or more times during one year

TABLE 2. Wildlife found in the State of Utah, the Uinta Basin, and Oil Shale Tracts Ua-Ub.

	Number of species		
	Utah	in Uinta Basin	Ua-Ub
AMPHIBIA			
Ambystomatidae	1	1	0
Pelobatidae	2	1	1
Bufonidae	5	1	2*
Hylidae	2	1	1
Ranidae	3	1	1
	13[1]	5[2]	5
REPTILIA			
Iguanidae	14	4	5*
Teiidae	3	1	1
Colubridae	19	6	4
Viperidae	5	1	1
	41[1]	12[2]	11
AVES			
Gaviiformes	3	1	0
Podicipediformes	8	6	0
Ciconiiformes	15	8	3
Anseriformes	37	25	14
Falconiformes	22	17	15
Galliformes	11	9	3
Gruiformes	7	6	3
Charadriiformes	53	36	6
Columbiformes	6	3	1
Cuculiformes	3	0	1*
Strigiformes	12	12	4
Caprimulgiformes	4	2	2
Apodiformes	11	5	4
Coraciiformes	1	1	1
Piciformes	11	9	4
Passeriformes	186	125	94*
	390[3]	265[4]	155
MAMMALIA			
Insectivora	4	2	0
Chiroptera	17	11	9*
Lagomorpha	7	6	2
Rodentia	61	31	20*
Carnivora	23	11	10
Artiodactyla	6	5	3
	118[5]	66[5,6]	44

*New record for the Uinta Basin
[1] Stebbins 1966
[2] Hayward et al. 1958, Olsen 1973
[3] Behle and Perry 1975, Hayward et al. 1976
[4] Behle 1981
[5] Durrant 1952
[6] Ranck 1961, Olsen 1973

Except for the short-horned lizard (*Phrynosoma douglassi*), lizards were abundant and ubiquitous. The eastern fence (*Sceloporus undulatus*) and tree lizards preferred the wooded habitats but occurred in a shallow-soiled shadscale vegetation abutting juniper woodlands on rugged topography present in western Ub and northern Ua. Where exposed sandstone was scattered, soils deeper, and juniper absent (in the shadscale vegetation in the eastern portion of Ub), both lizard species were absent. Rocks and trees served as hunting sites for these sit-and-wait predators. The sagebrush lizard (*Sceloporus graciosus*) preferred the three upland habitats over riparian vegetation. It foraged in open ground beneath the shrub canopy and in the bare interspace around shrubs. It was not found in dense grass cover and decreased in abundance from 1981 through 1983 ($p \leq 0.05$) as greater precipitation caused grass cover to increase. The side-blotched lizard (*Uta stansburiana*) foraged in the extensive bare ground and horizontal sandstone surfaces found in shadscale and juniper vegetation and was not found in the grassy areas. The western whiptail (*Cnemidophorous tigris*) demonstrated no habitat preference but was most often associated with greasewood, rabbitbrush, and sagebrush,

TABLE 3. Amphibian residency status, consistency, spatial distribution, and abundance in four vegetation types at Oil Shale Tracts Ua-Ub. Abbreviations are explained in Table 1.

ORDER Family Common name *Genus species*	Spatial distribution and abundance 1975–1984				
	Residency status	Years present	Month	Vegetation type	Number/ Kilometer ± SD
SALIENTIA					
Pelobatidae					
Great Basin Spadefoot	P	8	June	Gp	*
Scaphiopus intermontanus				Sp	*
				R	*
Bufonidae					
Woodhouse's Toad	P	9	June	Gp	*
Bufo woodhousei				Sp	*
				R	*
Red-spotted Toad	?	1	June	Gp	*
Bufo punctatus					
Hylidae					
Chorus Frog	?	3	June	R	*
Pseudacris triseriata					
Ranidae					
Leopard Frog	P	5	June	R	*
Rana pipiens					

where it foraged actively in the litter at a shrub's base. The whiptail lizard also avoided grassy areas.

During periods of high grass and forb cover, both the side-blotched and whiptail lizards were low (1975 and 1983) compared to peak abundance during the 1977 drought ($p \leq 0.05$). The eastern fence and tree lizards, both at low abundance during the 1977 drought, increased in 1983 ($p \leq 0.05$).

Aves

CICONIIFORMES AND ANSERIFORMES.—Seventeen species of herons and waterfowl occurred along the White River (Table 5). Only the great blue heron (*Ardea herodias*) and Canada goose (*Branta canadensis*) spent much time along the river. The herons foraged in the area surveyed in this study, but no nests were found. Abundance was lowest in April (Table 6). The geese nested on sandbars along the river banks and in sandstone cliffs separating riparian vegetation from shadscale vegetation. Adult geese were at peak abundance during April (Table 6). There were unpublished reports (J. Grandison, UDWR, Vernal, Utah, verbal communication) that these geese flew into southern Wyoming by August, then returned by October. These data support Grandison in that the only time geese stayed along the White was during the 1977 drought.

FALCONIFORMES.—Fifteen species of raptors occurred at Ua-Ub (Table 5). Most were observed during the nesting season in February and April (Table 6). Three raptors were permanent residents; of these, the golden eagle was the most abundant. During 1983 seven pairs of golden eagles successfully nested in the sandstone cliffs within 2 km (1.2 mi) perimeter of Ua-Ub. Two additional nests outside the perimeter were also successful in 1983. Five raptors were summer residents, and the red-tailed hawk (*Buteo jamaicensis*) and American kestrel (*Falco sparvarius*) were most abundant. Also during 1983 seven pairs of red-tailed hawks successfully nested in the same area as the eagles and two other successful red-tailed hawk nests occurred outside the perimeter. Most of the nests were in sandstone cliffs, except one, which occurred in a cottonwood tree along the White River. Kestrels were also abundant during 1976, 1982, and 1983, years of high rodent abundance. Red-tailed hawks and eagles both increased as rabbits increased in 1983; both eagles and rabbits decreased in 1984. The hawks also decreased in 1984, but not as drastically because they used other prey resources.

Among the three winter residents, the goshawk (*Accipiter gentilis*) arrived at Ua-Ub

TABLE 4. Reptilian residency status, consistency, spatial distribution, and abundance in four vegetation types at Oil Shale Tracts Ua-Ub. Abbreviations are explained in Table 1. Letters after abundance indicate differences at $p \leq 0.05$.

ORDER **Family** Common name *Genus species*	Residency status	Spatial distribution and abundance 1975–1984 Years present	 Month	 Vegetation type	 Number/ Kilometer ± SD
SQUAMATA					
Iguanidae					
Eastern Fence Lizard *Sceloporus undulatus*	P	10	June	G	0.08 a
				S	0.3 ± 0.3 b
				J	0.7 ± 0.4 c
				R	0.5 ± 0.5 bc
Sagebrush Lizard *Sceloporus graciosus*	P	10	June	G	1.9 ± 0.7 ab
				S	1.8 ± 0.8 a
				J	2.6 ± 1.6 b
				R	0.9 ± 0.6 c
Side-blotched Lizard *Uta stansburiana*	P	10	June	G	0.2 ± 0.1 a
				S	1.9 ± 1.7 b
				J	2.4 ± 1.2 b
				R	0.3 ± 0.5 a
Tree Lizard *Urosaurus ornata*	P	10	June	G	0.01 a
				S	0.1 ± 0.1 b
				J	0.5 ± 0.4 c
				R	0.3 ± 0.4 bc
Short-horned Lizard *Phrynosoma douglassi*	P	9	June	G	0.03
				S	0.08
				J	0.02
Teiidae					
Western Whiptail *Cnemidophorus tigris*	P	10	June	G	1.1 ± 0.5
				S	1.3 ± 1.0
				J	1.0 ± 0.7
				R	0.9 ± 0.9
Colubridae					
Racer *Coluber constrictor*	P	9	June	R	0.1 ± 0.1
Striped Whipsnake *Masticophis taeniatus*	P	9	June	G	0.01
				S	0.01
				J	*
				R	*
Gopher Snake *Pituophis melanoleucus*	P	10	June	G	0.01
				S	0.02
				J	0.03
				R	0.04
Western Terrestrial Garter Snake *Thamnophis elegans*	P	2	June	R	0.01
Viperidae					
Western Rattlesnake *Crotalus viridis*	P	10	June	G	0.1 ± 0.1
				S	0.02
				J	0.01
				R[1]	*

[1] Evacuation Creek exclusively

in October (Table 6) and roosted mainly in cottonwoods along the White River (Table 5). The rough-legged hawk (*Buteo lagopus*), though few in number at Ua-Ub, was numerous and consistently found in the open shrublands north and west of Ua-Ub. The ferruginous hawk (*Buteo regalis*), infrequently found at Ua-Ub, nested at low abundance and was a permanent resident during 1983 in the area north and west of Ua-Ub. The bald eagle

TABLE 5. Avian residency status, consistency, spatial distribution, and abundance in four vegetation types at Oil Shale Tracts Ua-Ub. Abbreviations are explained in Table 1. Letters after abundance indicate differences at $p \leq 0.05$.

ORDER	Spatial distribution and abundance 1975–1984				
Family Common name *Genus species*	Residency status	Years present	Month	Vegetation type	Number/ Kilometer ± SD
CICONIIFORMES					
Ardeidae					
Great Blue Heron	s	9	June	R	0.01
Ardea herodias					
Snowy Egret	m	1	April	R	*
Egretta thula					
Black-crowned Night Heron	m	1	April	R	*
Nycticorax nycticorax					
ANSERIFORMES					
Anatidae					
Canada Goose	S	10	April	R	2.0 ± 1.0
Branta canadensis					
Green-winged Teal	m	9	April	Gp	*
Anas crecca				R	0.2 ± 0.3
Mallard	m	10	April	Gp	*
Anas platyrhynchos				R	0.1 ± 0.2
Pintail	m	2	April	R	*
Anas acuta					
Blue-winged Teal	m	5	April	R	*
Anas discors					
Cinnamon Teal	m	4	April	R	0.04
Anas cyanoptera					
Northern Shoveler	m	4	April	R	*
Anas clypeata					
Gadwall	m	4	April	R	*
Anas strepera					
American Wigeon	m	3	April	R	*
Anas americana					
Ring-necked Duck	m	1	April	R	*
Aythya collaris					
Lesser Scaup	m	1	April	R	*
Aythya affinis					
Bufflehead	m	1	April	R	*
Bucephala albeola					
Common Merganser	w	10	April	R	0.1 ± 0.3
Mergus merganser					
Red-breasted Merganser	m	2	April	R	0.08
Mergus serrator					
FALCONIFORMES					
Cathartidae					
Turkey Vulture	S	10	April	G	*
Cathartes aura				S	0.1 ± 0.2
				J	*
				R	0.4 ± 0.7
Accipitridae					
Bald Eagle	w	10	February	S	*
Haliaeetus leucocephalus				R	0.2 ± 0.2
Northern Harrier	P	10	April	G	*
Circus cyaneus				S	0.02
				R	*

Table 5 continued.

ORDER **Family** Common name *Genus species*	Spatial distribution and abundance 1975–1984					
	Residency status	Years present	Month	Vegetation type	Number/ Kilometer ± SD	
Sharp-shinned Hawk	?	7	June	J	*	
Accipiter striatus				R	0.01	
Cooper's Hawk	S,P	9	April	G	*	
Accipiter cooperii				J	*	
				R	0.2 ± 0.4	
Northern Goshawk	w	6	February	J	*	
Accipiter gentilis				R	0.2 ± 0.1	
Swainson's Hawk	m	2	August	G	0.01	
Buteo swainsoni				S	*	
Red-tailed Hawk	S,P	10	June	G	0.03	
Buteo jamaicensis				S	0.1 ± 0.1	
				J	0.06	
				R	0.4 ± 0.6	
Ferruginous Hawk	m	1	October	J	*	
Buteo regalis						
Rough-legged Hawk	w	5	February	G	*	
Buteo lagopus				S	*	
				J	*	
				R	0.02	
Golden Eagle	P	10	February	G	0.3 ± 0.2	
Aquila chrysaetos				S	0.06	
				J	0.1 ± 0.2	
				R	0.01	
Falconidae						
American Kestrel	S	10	June	G	0.1 ± 0.2	a
Falco sparverius				S	0.09	a
				J	0.09	a
				R	0.4 ± 0.4	b
Merlin	m	1	August	R	0.01	
Falco columbarius						
Peregrine Falcon	m	1	April	G	*	
Falco peregrinus				R	*	
Prairie Falcon	P	10	June	G	0.03	
Falco mexicanus				S	*	
				J	*	
				R	0.03	
GALLIFORMES						
Phasianidae						
Chukar	t	3	June	G	*	
Alectoris chukar				R	0.1 ± 0.3	
Sage Grouse	t	1	April	S	*	
Centrocercus urophasianus						
Ring-necked Pheasant	t	4	June	G	*	
Phasianus colchicus				R	*	
GRUIFORMES						
Rallidae						
Virginia Rail	?	2	June	Gp	*	
Rallus limicola						
Gruidae						
Sandhill Crane	m	10	April	R	0.02	
Grus canadensis						

Table 5 continued.

Order Family Common name *Genus species*	Spatial distribution and abundance 1975–1984					
	Residency status	Years present	Month	Vegetation type	Number/ Kilometer ± SD	
Whooping Crane	m	1	October	Flying over Ua-Ub	*	
Grus americana						
Charadriiformes						
Charadriidae						
Killdeer	S	10	June	Gp	*	
Charadrius vociferus				S	0.02	
				R	0.02	
Recurvirostridae						
American Avocet	m	3	April	R	*	
Recurvirostra americana						
Scolopacidae						
Greater Yellowlegs	m	4	April	R	0.01	
Tringa melanoleuca						
Solitary Sandpiper	s	2	June	R	*	
Tringa solitaria						
Spotted Sandpiper	S	10	June	R	0.9 ± 0.8	
Actitis macularia						
Common Snipe	m	1	April	R	*	
Gallinago gallinago						
Columbiformes						
Columbidae						
Mourning Dove	S	10	June	G	0.5 ± 0.4	a
Zenaida macroura				S	0.4 ± 0.3	a
				J	0.9 ± 0.6	
				R	1.4 ± 1.2	b
Cuculiformes						
Cuculidae						
Yellow-billed Cuckoo	s	2	June	R	0.02	
Coccyzus americanus						
Strigiformes						
Strigidae						
Western Screech-Owl	t	2	April	J	*	
Otus kennicottii				R	*	
Great Horned Owl	P	10	June	G	*	
Bubo virginianus				S	*	
				J	*	
				R	0.2 ± 0.3	
Long-eared Owl	P	6	April	R	*	
Asio otus						
Short-eared Owl	t	4	April	S	*	
Asio flammeus				J	*	
				R	*	
Caprimulgiformes						
Caprimulgidae						
Common Nighthawk	S	10	June	G	0.2 ± 0.3	
Chordeiles minor				S	0.4 ± 0.5	
				J	0.5 ± 0.7	
				R	0.2 ± 0.2	
Common Poorwill	S	10	June	G	*	
Phalaenoptilus nuttallii				S	*	
				J	0.05	
Apodiformes						
Apodidae						
White-throated Swift	S	10	June	G	0.08	
Aeronautes saxatalis				S	0.2 ± 0.4	
				J	0.08	
				R	0.4 ± 0.5	

Table 5 continued.

ORDER **Family** Common name *Genus species*	Spatial distribution and abundance 1975–1984 Residency status	Years present	Month	Vegetation type	Number/ Kilometer ± SD
Trochilidae					
Black-chinned Hummingbird	S	6	June	G	0.01
Archilochus alexandri				J	0.2 ± 0.5
				R	0.01
Broad-tailed Hummingbird	S	8	June	G	0.01
Selasphorus platycercus				S	0.01
				J	0.01
				R	0.2 ± 0.3
Rufous Hummingbird	m	1	August	R	*
Selasphorus rufus					
CORACIIFORMES					
Alcedinidae					
Belted Kingfisher	t	8	April	R	0.05
Ceryle alcyon					
PICIFORMES					
Picidae					
Yellow-bellied Sapsucker	t	3	October	R	0.3 ± 0.4
Sphyrapicus varius					
Downy Woodpecker	P	10	June	R	0.3 ± 0.5
Picoides pubescens					
Hairy Woodpecker	p	10	June	R	0.06
Picoides villosus					
Northern Flicker	P	10	June	G	0.04
Colaptes auratus				S	0.01
				J	0.03
				R	0.9 ± 0.6
PASSERIFORMES					
Tyrannidae					
Olive-sided Flycatcher	m	1	August	R	0.02
Contopus borealis					
Western Wood Peewee	S	10	June	G	*
Contopus sordidulus				J	0.07
				R	0.4 ± 0.5
Willow Flycatcher	S	10	June	R	0.5 ± 0.5
Empidonax traillii					
Gray Flycatcher	S	10	June	G	0.2 ± 0.2 a
Empidonax wrightii				J	1.3 ± 0.5 b
				R	0.02 a
Eastern Phoebe	m	3	August	G	*
Sayornis phoebe				J	*
				R	*
Say's Phoebe	S	10	June	G	0.3 ± 0.2
Sayornis saya				S	0.2 ± 0.3
				J	0.2 ± 0.2
				R	0.2 ± 0.4
Ash-throated Flycatcher	S	10	June	G	0.1 ± 0.2 a
Myiarchus cinerascens				S	0.04 a
				J	0.08 a
				R	1.0 ± 0.8 b
Western Kingbird	S	9	June	G	0.01
Tyrannus verticalis				S	0.01
				R	0.2 ± 0.3

Table 5 continued.

ORDER	Spatial distribution and abundance 1975–1984					
Family Common name *Genus species*	Residency status	Years present	Month	Vegetation type	Number/ Kilometer ± SD	
Eastern Kingbird	s	3	June	G	0.01	
Tyrannus tyrannus				R	0.03	
Alaudidae						
Horned Lark	P	10	June	G	*	
Eremophila alpestris				S	0.01	
Hirundinidae						
Tree Swallow	t	3	June	Gp	*	
Tachycineta bicolor				J	*	
				R	*	
Violet-green Swallow	S	10	June	G	0.1 ± 0.2	
Tachycineta thalassina				S	0.04	
				J	0.2 ± 0.4	
				R	0.04	
Northern Rough-winged	s	6	June	S	*	
Swallow				J	0.02	
Stelgidopteryx serripennis				R	0.04	
Cliff Swallow	S	10	June	G	0.02	
Hirundo pyrrhonota				S	0.7 ± 1.3	
				J	0.07	
				R	30.4 ± 33.0	
Barn Swallow	m,s	10	June	S	*	
Hirundo rustica				J	*	
				R	0.01	
Corvidae						
Scrub Jay	P	8	June	G	*	
Aphelocoma coerulescens				J	0.01	
				R	*	
Pinyon Jay	P	10	April	G	2.9 ± 3.8	a
Gymnorhinus cyanocephalus				S	0.09	a
				J	7.2 ± 5.6	b
Clark's Nutcracker	t	3	April	J	*	
Nucifraga columbiana				R	*	
Black-billed Magpie	P	10	June	G	0.4 ± 0.6	a
Pica pica				S	0.01	a
				J	0.2 ± 0.3	a
				R	1.4 ± 1.3	b
Common Crow	t	4	April	G	0.01	
Corvus brachyrhynchos				R	0.01	
Common Raven	P	10	February	G	0.6 ± 0.6	
Corvus corax				S	0.04	
				J	0.2 ± 0.2	
				R	0.3 ± 0.2	
Paridae						
Black-capped Chickadee	P	10	June	G	*	
Parus atricapillus				J	*	
				R	0.7 ± 0.5	
Mountain Chickadee	w	6	October	G	*	
Parus gambeli				J	0.08	
				R	0.2 ± 0.5	
Plain Titmouse	P	10	June	G	0.1 ± 0.2	
Parus inornatus				J	0.4 ± 0.5	
Aegithalidae						
Bushtit	w	6	February	J	*	
Psaltriparus minimus				R	*	

Table 5 continued.

ORDER **Family** Common name *Genus species*	Spatial distribution and abundance 1975–1984				
	Residency status	Years present	Month	Vegetation type	Number/ Kilometer ± SD
Sittidae					
Red-breasted Nuthatch	t	4	August	J	0.01
Sitta canadensis				R	0.04
White-breasted Nuthatch	t,w	5	August	R	0.1 ± 0.2
Sitta carolinensis					
Certhiidae					
Brown Creeper	w	4	October	R	0.2 ± 0.2
Certhia americana					
Troglodytidae					
Rock Wren	S	10	June	G	1.7 ± 0.8 a
Salpinctes obsoletus				S	1.0 ± 0.5 bc
				J	1.2 ± 0.5 c
				R	0.5 ± 0.8 b
Canyon Wren	P	9	June	G	0.01
Catherpes mexicanus				S	*
				J	0.06
				R	*
Bewick's Wren	S	9	June	G	*
Thryomanes bewickii				J	0.2 ± 0.3
				R	*
House Wren	S	10	June	R	0.8 ± 0.8
Troglodytes aedon					
Marsh Wren	S	6	June	Gp	*
Cistothorus palustris					
Muscicapidae					
Ruby-crowned Kinglet	m	9	October	G	0.04
Regulus calendula				J	0.04
				R	0.8 ± 1.0
Blue-gray Gnatcatcher	S	10	June	G	0.07 a
Polioptila caerulea				S	0.01 a
				J	0.8 ± 0.7 b
				R	1.5 ± 0.7 c
Black-tailed Gnatcatcher	s	1	June	G	0.01
Polioptila melanura				J	0.01
				R	0.1 ± 0.3
Western Bluebird	m	2	April	R	0.04
Sialia mexicana					
Mountain Bluebird	S,P	10	June	G	1.0 ± 1.4
Sialia currucoides				S	0.1 ± 0.2
				J	0.7 ± 0.6
				R	1.3 ± 1.6
Townsend's Solitaire	m	8	April	G	0.01
Myadestes townsendi				J	0.01
				R	0.2 ± 0.4
Swainson's Thrush	m	3	October	R	0.01
Catharus ustulatus					
Hermit Thrush	m	4	October	R	0.01
Catharus guttatus					
American Robin	S	10	June	G	*
Turdus migratorius				J	*
				R	1.7 ± 0.9

Table 5 continued.

ORDER Family Common name *Genus species*	Spatial distribution and abundance 1975–1984				
	Residency status	Years present	Month	Vegetation type	Number/ Kilometer ± SD
Mimidae					
Gray Catbird	?	1	June	R	*
Dumetella carolinensis					
Northern Mockingbird	S	5	June	G	0.2 ± 0.5
Mimus polyglottos				S	0.01
				R	0.01
Sage Thrasher	S	10	June	G	0.01
Oreoscoptes montanus				S	0.3 ± 0.3
				J	0.01
Bendire's Thrasher	?	1	June	S	*
Toxostoma bendirei					
Motacillidae					
Water Pipit	m	3	April	S	0.01
Anthus spinoletta				R	*
Bombycillidae					
Cedar Waxwing	s	7	June	R	1.3 ± 1.9
Bombycilla cedrorum					
Laniidae					
Northern Shrike	w	3	February	G	*
Lanius excubitor				S	*
				R	0.01
Loggerhead Shrike	P,S	10	June	G	0.4 ± 0.6
Lanius ludovicianus				S	0.4 ± 0.6
				J	0.05
Sturnidae					
European Starling	S	10	June	G	0.1 ± 0.3
Sturnus vulgaris				S	0.01
				J	0.01
				R	1.8 ± 1.8
Vireonidae					
Gray Vireo	s	1	June	J	*
Vireo vicinior					
Solitary Vireo	S	8	June	J	*
Vireo solitarius				R	0.3 ± 0.4
Warbling Vireo	S	9	June	R	0.4 ± 0.6
Vireo gilvus					
Red-eyed Vireo	?	2	June	R	0.03
Vireo olivaceus					
Emberizidae					
Orange-crowned Warbler	s	6	June	R	0.07
Vermivora celata					
Virginia's Warbler	s	2	June	R	0.2 ± 0.5
Vermivora virginiae					
Yellow Warbler	S	10	June	R	5.5 ± 1.9
Dendroica petechia					
Yellow-rumped Warbler	m,s	10	October	G	0.1 ± 0.2
Dendroica coronata				J	0.07
				R	0.5 ± 0.7
Black-throated Gray Warbler	S	10	June	G	0.1 ± 0.1 a
Dendroica nigrescens				J	1.8 ± 1.2 b
				R	0.04 a

Table 5 continued.

ORDER Family Common name *Genus species*	Spatial distribution and abundance 1975–1984				
	Residency status	Years present	Month	Vegetation type	Number/ Kilometer ± SD
Townsend's Warbler *Dendroica townsendi*	m	2	August	R	0.2 ± 0.4
MacGillivray's Warbler *Oporornis tolmiei*	s	3	June	R	0.03
Common Yellowthroat *Geothlypis trichas*	s	5	June	R	0.04
Wilson's Warbler *Wilsonia pusilla*	m	5	October	R	0.04
Yellow-breasted Chat *Icteria virens*	S	10	June	R	1.1 ± 0.5
Western Tanager *Piranga ludoviciana*	S	9	June	G	0.01
				J	0.05
				R	1.3 ± 1.7
Rose-breasted Grosbeak *Pheucticus ludovicianus*	?	2	June	J	*
				R	0.01
Black-headed Grosbeak *Pheucticus melanocephalus*	S	7	June	G	0.01
				R	0.4 ± 0.4
Blue Grosbeak *Guiraca caerulea*	S	8	June	R	0.3 ± 0.5
Lazuli Bunting *Passerina amoena*	S	8	June	G	0.01
				R	1.3 ± 1.3
Green-tailed Towhee *Pipilo chlorurus*	m	4	April	G	0.03
				R	0.09
Rufous-sided Towhee *Pipilo erythrophthalmus*	S	10	June	G	0.02
				J	*
				R	3.1 ± 1.4
American Tree Sparrow *Spizella arborea*	w	2	February	R[1]	0.7 ± 1.8
Chipping Sparrow *Spizella passerina*	S	10	June	G	0.4 ± 0.7 a
				J	1.0 ± 0.8 b
				R	0.09 a
Brewer's Sparrow *Spizella breweri*	S	10	June	G	2.2 ± 2.4 a
				S	0.8 ± 1.0 b
				J	0.1 ± 0.2 b
				R	0.2 ± 0.5 b
Vesper Sparrow *Pooecetes gramineus*	m	9	April	G	0.4 ± 0.9
				S	0.2 ± 0.3
Lark Sparrow *Chondestes grammacus*	S	10	June	G	0.5 ± 0.5 ac
				S	1.1 ± 0.8 b
				J	0.2 ± 0.3 a
				R	0.9 ± 0.7 bc
Black-throated Sparrow *Amphispiza bilineata*	S	10	June	G	1.9 ± 0.6 a
				S	1.2 ± 0.7 b
				J	0.7 ± 0.6 b
				R	0.04 c
Sage Sparrow *Amphispiza belli*	S	10	June	G	0.3 ± 0.2 a
				S	1.8 ± 1.2 b
				J	*
				R	*

Table 5 continued.

ORDER **Family** Common name *Genus species*	Spatial distribution and abundance 1975–1984				
	Residency status	Years present	Month	Vegetation type	Number/ Kilometer ± SD
Savannah Sparrow *Passerculus sandwichensis*	m	1	June	S	*
Song Sparrow *Melospiza melodia*	p	9	June	Gp	*
				R	0.01
White-crowned Sparrow *Zonotrichia leucophrys*	m,s	10	April	G	0.2 ± 0.4
				S	*
				J	*
				R	0.6 ± 1.0
Dark-eyed Junco *Junco hyemalis*	w	10	April	G	4.4 ± 6.4
				S	0.1 ± 0.3
				J	4.2 ± 5.9
				R	3.4 ± 5.8
Red-winged Blackbird *Agelaius phoeniceus*	S	10	June	G	0.04
				R	0.06
Western Meadowlark *Sturnella neglecta*	S	10	June	G	0.9 ± 0.9 a
				S	1.8 ± 1.0 b
				J	0.02 c
				R	0.3 ± 0.3 c
Brewer's Blackbird *Euphagus cyanocephalus*	s	10	June	G	0.2 ± 0.8
				S	0.02
				J	0.1 ± 0.2
				R	0.1 ± 0.3
Brown-headed Cowbird *Molothrus ater*	S	10	June	G	0.01 a
				J	0.6 ± 0.8 a
				R	4.4 ± 1.7 b
Northern Oriole *Icterus galbula*	S	10	June	R	2.0 ± 1.3
Scott's Oriole *Icterus parisorum*	S	8	June	G	0.08
				J	0.02
Fringillidae					
Rosy Finch *Leucosticte arctoa*	w	9	February	G	1.5 ± 4.0
				S	0.1 ± 0.4
				J	1.7 ± 4.5
				R	4.8 ± 12.6
House Finch *Carpodacus mexicanus*	S,P	10	June	G	0.5 ± 0.4 a
				S	0.4 ± 0.7 a
				J	2.5 ± 1.6 a
				R	6.1 ± 5.9 b
Pine Siskin *Carduelis pinus*	w	4	April	G	0.04
				S	*
				J	*
				R	*
Lesser Goldfinch *Carduelis psaltria*	?	1		R	*
American Goldfinch *Carduelis tristis*	S	8	June	J	0.01
				R	0.3 ± 0.5

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[1] Evacuation Creek exclusively

TABLE 6. Avian seasonal distribution and abundance in four vegetation types at Oil Shale Tracts Ua-Ub. Abbreviations are explained in Table 1.

		Seasonal distribution and abundance 1975–1981				
		Number/Kilometer ± SD				
Common name	Vegetation Type	February	April	June	August	October
Great Blue Heron	R	—	*	< 0.1	< 0.1	< 0.1
Canada Goose	R	0.3 ± 0.8	2.1 ± 1.0	0.2 ± 0.4	0.2 ± 0.5	0.7 ± 1.1
Green-winged Teal	R	—	0.2 ± 0.3	< 0.1	< 0.1	—
Mallard	R	*	0.1 ± 0.2	*	< 0.1	*
Cinnamon Teal	R	—	< 0.1	< 0.1	—	—
Common Merganser	R	< 0.1	0.1 ± 0.3	—	—	*
Turkey Vulture	G	—	*	*	*	—
	S	—	< 0.1	*	*	—
	J	—	*	*	—	—
	R	—	0.5 ± 0.8	0.2 ± 0.7	< 0.1	—
Bald Eagle	G	*	—	—	—	—
	S	*	—	—	—	—
	R	0.2 ± 0.2	—	—	—	—
Northern Harrier	G	—	*	*	*	*
	S	< 0.1	< 0.1	*	*	< 0.1
	J	*	*	*	*	*
	R	*	—	*	*	*
Cooper's Hawk	G	< 0.1	*	—	*	—
	S	*	—	—	—	*
	J	*	*	*	—	—
	R	*	0.2 ± 0.4	< 0.1	< 0.1	< 0.1
Goshawk	G	—	*	—	—	*
	J	*	*	—	—	*
	R	0.2 ± 0.1	—	—	—	*
Red-tailed Hawk	G	< 0.1	*	< 0.1	*	*
	S	*	< 0.1	< 0.1	*	*
	J	*	*	< 0.1	< 0.1	< 0.1
	R	0.1 ± 0.3	< 0.1	< 0.1	< 0.1	< 0.1
Rough-legged Hawk	G	*	—	—	—	*
	S	*	—	—	—	—
	J	*	—	—	—	—
	R	< 0.1	—	—	—	—
Golden Eagle	G	0.4 ± 0.2	< 0.1	< 0.1	< 0.1	0.1 ± 0.1
	S	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1
	J	0.1 ± 0.2	*	< 0.1	*	*
	R	< 0.1	0.1 ± 0.2	0.1 ± 0.1	0.1 ± 0.2	< 0.1
American Kestrel	G	—	0.2 ± 0.2	< 0.1	0.1 ± 0.1	*
	S	*	0.2 ± 0.1	< 0.1	0.2 ± 0.3	< 0.1
	J	—	< 0.1	0.1 ± 0.1	< 0.1	*
	R	—	0.6 ± 0.3	0.2 ± 0.2	0.1 ± 0.4	*
Prairie Falcon	G	—	*	< 0.1	*	*
	S	< 0.1	—	*	*	*
	J	*	*	*	*	*
	R	*	—	< 0.1	*	*
Killdeer	S	—	*	*	*	—
	R	—	0.1 ± 0.2	< 0.1	0.1 ± 0.3	—
Spotted Sandpiper	R	—	—	1.0 ± 0.9	0.4 ± 0.5	—
Mourning Dove	G	—	0.2 ± 0.2	0.5 ± 0.5	2.1 ± 3.5	*
	S	—	< 0.1	0.4 ± 0.4	0.4 ± 0.5	*
	J	—	0.1 ± 0.3	1.0 ± 0.6	0.6 ± 0.6	*
	R	—	0.6 ± 0.5	1.5 ± 1.5	4.3 ± 5.4	0.2 ± 0.3
Great Horned Owl	G	*	—	*	*	*
	S	*	*	*	—	*
	J	< 0.1	*	*	< 0.1	*
	R	0.2 ± 0.2	< 0.1	0.2 ± 0.3	0.2 ± 0.2	*

Table 6 continued.

		Seasonal distribution and abundance 1975–1981				
		Number/Kilometer ± SD				
Common name	Vegetation Type	February	April	June	August	October
Common Nighthawk	G	—	—	0.3 ± 0.4[1]	0.3 ± 0.4[1]	—
	S	—	—	0.5 ± 0.6[1]	0.7 ± 0.8[1]	—
	J	—	—	0.8 ± 0.7[1]	0.5 ± 0.8[1]	—
	R	—	—	0.2 ± 0.3[1]	9.1 ± 12.1[1]	—
White-throated Swift	G	—	—	< 0.1	*	—
	S	—	< 0.1	0.2 ± 0.4	*	*
	J	—	0.1 ± 0.3	< 0.1	< 0.1	—
	R	—	0.1 ± 0.3	0.2 ± 0.2	0.2 ± 0.5	*
Black-chinned Hummingbird	G	—	—	< 0.1	—	—
	J	—	—	0.1 ± 0.1	< 0.1	—
	R	—	—	< 0.1	—	—
Broad-tailed Hummingbird	S	—	—	< 0.1	< 0.1	—
	R	—	< 0.1	< 0.1	0.2 ± 0.3	—
Belted Kingfisher	R	—	< 0.1	—	—	< 0.1
Hairy Woodpecker	R	0.1 ± 0.2	0.1 ± 0.2	< 0.1	0.2 ± 0.3	0.2 ± 0.3
Downy Woodpecker	R	0.2 ± 0.2	0.4 ± 0.4	0.2 ± 0.2	0.1 ± 0.1	0.1 ± 0.1
Northern Flicker	G	< 0.1	0.1 ± 0.2	< 0.1	< 0.1	0.2 ± 0.2
	S	—	< 0.1	< 0.1	—	—
	J	*	0.2 ± 0.5	< 0.1	< 0.1	0.1 ± 0.2
	R	< 0.1	1.3 ± 1.0	0.8 ± 0.7	1.0 ± 1.2	0.6 ± 0.1
Western Wood Peewee	G	—	< 0.1	*	—	—
	J	—	0.1 ± 0.2	< 0.1	0.1 ± 0.2	—
	R	—	—	0.3 ± 0.3	0.2 ± 0.3	—
Willow Flycatcher	R	—	< 0.1	0.3 ± 0.2	0.1 ± 0.2	—
Gray Flycatcher	G	—	—	0.3 ± 0.2	0.1 ± 0.2	—
	J	—	< 0.1	1.2 ± 0.4	0.2 ± 0.1	—
	R	—	—	< 0.1	*	—
Say's Phoebe	G	—	0.4 ± 0.4	0.2 ± 0.2	0.6 ± 0.5	< 0.1
	S	*	0.1 ± 0.2	0.1 ± 0.2	< 0.1	—
	J	—	0.1 ± 0.1	0.2 ± 0.2	0.2 ± 0.2	—
	R	—	0.8 ± 1.0	< 0.1	0.3 ± 0.4	—
Ash-throated Flycatcher	G	—	—	< 0.1	< 0.1	—
	S	—	—	—	—	—
	J	—	—	< 0.1	0.1 ± 0.2	—
	R	—	—	0.6 ± 0.7	0.2 ± 0.4	—
Western Kingbird	G	—	< 0.1	< 0.1	*	—
	S	—	*	< 0.1	—	—
	R	—	—	< 0.1	< 0.1	—
Horned Lark	G	0.7 ± 1.0	*	*	—	0.4 ± 0.8
	S	4.6 ± 5.2	< 0.1	< 0.1	< 0.1	8.7 ± 9.1
	J	*	—	*	< 0.1	< 0.1
	R	< 0.1	—	—	—	2.0 ± 3.7
Violet-green Swallow	G	—	—	< 0.1	0.1 ± 0.2	—
	S	—	—	< 0.1	*	—
	J	—	—	0.1 ± 0.3	*	—
	R	—	< 0.1	< 0.1	0.2 ± 0.3	—
Northern Rough-winged Swallow	G	—	—	*	*	—
	S	—	—	—	0.3 ± 0.6	—
	J	—	—	< 0.1	—	—
	R	—	*	< 0.1	0.6 ± 0.7	—
Cliff Swallow	G	—	—	< 0.1	—	—
	S	—	—	*	< 0.1	—
	J	—	—	0.1 ± 0.2	—	—
	R	—	—	18.5 ± 17.6	0.4 ± 0.7	—
Barn Swallow	G	—	—	—	*	—
	S	—	—	—	—	< 0.1
	J	—	*	—	—	*
	R	—	*	*	*	< 0.1

Table 6 continued.

Common name	Vegetation Type	Seasonal distribution and abundance 1975–1981				
		Number/Kilometer ± SD				
		February	April	June	August	October
Scrub Jay	G	< 0.1	*	*	< 0.1	*
	J	*	< 0.1	< 0.1	< 0.1	*
	R	—	< 0.1	*	< 0.1	0.1 ± 0.3
Pinyon Jay	G	3.6 ± 7.6	2.2 ± 2.6	1.7 ± 1.8	3.0 ± 2.7	5.5 ± 6.9
	S	—	0.1 ± 0.3	0.1 ± 0.3	1.2 ± 2.2	< 0.1
	J	1.1 ± 2.1	5.1 ± 3.7	1.1 ± 1.6	1.5 ± 2.6	5.0 ± 4.7
	R	*	—	—	< 0.1	—
Black-billed Magpie	G	0.9 ± 1.1	0.4 ± 0.4	0.6 ± 0.7	< 0.1	0.4 ± 0.3
	S	*	< 0.1	< 0.1	< 0.1	< 0.1
	J	0.2 ± 0.3	< 0.1	0.3 ± 0.3	< 0.1	0.2 ± 0.2
	R	1.1 ± 1.2	0.9 ± 0.6	2.0 ± 1.2	1.0 ± 1.2	1.8 ± 2.0
Common Raven	G	0.7 ± 0.6	< 0.1	*	*	*
	S	< 0.1	*	*	< 0.1	*
	J	0.3 ± 0.2	< 0.1	< 0.1	—	—
	R	0.3 ± 0.2	< 0.1	*	*	—
Black-capped Chickadee	G	< 0.1	—	—	—	0.2 ± 0.4
	J	*	—	—	—	< 0.1
	R	0.6 ± 0.6	0.4 ± 0.3	0.7 ± 0.6	1.1 ± 1.2	2.3 ± 2.0
Mountain Chickadee	G	< 0.1	—	—	—	*
	J	0.1 ± 0.3	—	—	—	< 0.1
	R	—	—	—	—	0.2 ± 0.5
Plain Titmouse	G	< 0.1	0.1 ± 0.2	0.1 ± 0.3	< 0.1	< 0.1
	J	0.3 ± 0.3	0.5 ± 0.4	0.4 ± 0.5	0.4 ± 0.5	0.4 ± 0.3
	R	—	—	—	—	*
Bushtit	J	*	< 0.1	< 0.1	—	—
	R	—	—	—	—	0.4 ± 0.8
Rock Wren	G	—	0.7 ± 0.6	1.8 ± 1.0	2.2 ± 1.2	0.2 ± 0.3
	S	—	0.4 ± 0.4	1.0 ± 0.6	0.7 ± 0.3	< 0.1
	J	—	0.4 ± 0.5	1.1 ± 0.5	0.7 ± 0.4	0.1 ± 0.2
	R	—	0.1 ± 0.2	0.7 ± 0.9	1.0 ± 1.2	*
Canyon Wren	G	*	*	< 0.1	< 0.1	—
	S	< 0.1	—	—	—	—
	J	*	—	< 0.1	< 0.1	*
	R	*	*	*	*	*
Bewick's Wren	G	—	< 0.1	—	< 0.1	< 0.1
	J	—	0.1 ± 0.2	0.1 ± 0.3	< 0.1	*
	R	< 0.1	< 0.1	—	—	—
House Wren	G	—	—	—	*	—
	R	—	< 0.1	0.4 ± 0.4	< 0.1	—
Ruby-crowned Kinglet	G	—	—	—	*	< 0.1
	J	—	—	—	< 0.1	< 0.1
	R	—	*	—	—	0.9 ± 1.0
Blue-gray Gnatcatcher	G	—	< 0.1	< 0.1	< 0.1	—
	S	—	< 0.1	—	—	—
	J	—	*	0.9 ± 0.8	0.1 ± 0.1	—
	R	—	0.2 ± 0.4	1.3 ± 0.7	1.2 ± 0.6	< 0.1
Black-tailed Gnatcatcher	G	—	—	< 0.1	—	—
	J	—	—	< 0.1	—	—
	R	—	< 0.1	0.2 ± 0.4	< 0.1	—
Mountain Bluebird	G	< 0.1	1.1 ± 1.0	1.2 ± 1.6	0.5 ± 0.7	1.9 ± 2.1
	S	—	0.6 ± 1.1	0.1 ± 0.2	0.1 ± 0.2	1.0 ± 2.1
	J	—	0.7 ± 0.4	0.8 ± 0.7	0.7 ± 0.5	0.8 ± 0.4
	R	< 0.1	0.4 ± 0.4	0.6 ± 0.8	0.1 ± 0.3	0.4 ± 0.9
Townsend's Solitaire	G	—	*	—	—	—
	J	—	< 0.1	—	—	—
	R	—	0.2 ± 0.4	—	—	< 0.1

Table 6 continued.

		Seasonal distribution and abundance 1975–1981				
		Number/Kilometer ± SD				
Common name	Vegetation Type	February	April	June	August	October
American Robin	G	—	0.1 ± 0.1	—	*	—
	S	—	*	—	—	—
	J	< 0.1	0.1 ± 0.3	—	—	—
	R	< 0.1	2.6 ± 1.7	1.4 ± 0.6	0.3 ± 0.3	0.3 ± 0.5
Northern Mockingbird	G	—	—	0.2 ± 0.6	*	—
	S	—	—	*	—	—
Sage Thrasher	G	—	*	< 0.1	0.2 ± 0.3	*
	S	—	0.5 ± 0.3	0.4 ± 0.3	0.2 ± 0.2	< 0.1
	J	—	*	< 0.1	—	—
Cedar Waxwing	R	—	—	0.7 ± 1.2	—	—
Loggerhead Shrike	G	*	0.2 ± 0.3	0.3 ± 0.4	0.2 ± 0.2	< 0.1
	S	*	0.2 ± 0.2	0.6 ± 0.6	0.6 ± 0.3	0.1 ± 0.1
	J	< 0.1	*	< 0.1	< 0.1	< 0.1
	R	*	—	—	*	—
European Starling	G	—	—	0.1 ± 0.4	—	*
	S	—	< 0.1	*	*	*
	J	—	—	< 0.1	—	—
	R	—	2.6 ± 2.9	0.7 ± 0.5	*	*
Solitary Vireo	J	—	—	—	< 0.1	—
	R	—	—	0.2 ± 0.2	< 0.1	—
Warbling Vireo	R	—	—	0.2 ± 0.2	0.1 ± 0.2	—
Yellow Warbler	G	—	—	*	—	—
	S	—	—	*	—	—
	R	—	—	5.1 ± 2.0	1.4 ± 1.1	—
Yellow-rumped Warbler	G	—	—	*	—	0.1 ± 0.2
	S	—	< 0.1	—	—	—
	J	—	—	*	—	< 0.1
	R	—	0.4 ± 0.5	0.1 ± 0.2	—	0.5 ± 0.7
Black-throated Gray Warbler	G	—	—	0.1 ± 0.1	—	—
	J	—	0.2 ± 0.4	1.4 ± 0.6	< 0.1	—
	R	—	< 0.1	< 0.1	0.1 ± 0.2	—
Yellow-breasted Chat	R	—	—	1.1 ± 0.6	0.2 ± 0.2	—
Western Tanager	G	—	—	< 0.1	—	—
	J	—	—	< 0.1	*	—
	R	—	—	0.5 ± 0.4	< 0.1	—
Black-headed Grosbeak	R	—	—	0.3 ± 0.4	0.1 ± 0.3	—
Blue Grosbeak	R	—	—	0.1 ± 0.2	0.2 ± 0.4	—
Lazuli Bunting	G	—	—	*	—	—
	J	—	—	*	—	—
	R	—	—	0.9 ± 1.1	0.1 ± 0.3	—
Green-tailed Towhee	G	—	< 0.1	—	—	< 0.1
	R	—	0.1 ± 0.3	—	< 0.1	—
Rufous-sided Towhee	G	—	< 0.1	< 0.1	< 0.1	< 0.1
	S	—	—	—	< 0.1	—
	J	—	< 0.1	—	—	—
	R	*	2.1 ± 1.4	2.9 ± 1.7	1.4 ± 1.0	0.3 ± 0.6
American Tree Sparrow	R	0.8 ± 1.9[2]	—	—	—	< 0.1[2]
Chipping Sparrow	G	—	< 0.1	0.5 ± 0.8	0.2 ± 0.4	< 0.1
	S	—	< 0.1	—	—	—
	J	—	0.2 ± 0.5	0.8 ± 0.9	0.7 ± 1.2	< 0.1
	R	—	—	0.1 ± 0.3	0.2 ± 0.4	< 0.1
Brewer's Sparrow	G	—	0.4 ± 0.8	1.3 ± 1.8	1.1 ± 2.4	—
	S	—	< 0.1	0.6 ± 1.0	0.1 ± 0.2	—
	J	—	—	0.1 ± 0.2	0.2 ± 0.4	—
	R	—	*	0.2 ± 0.6	0.9 ± 1.8	—
Vesper Sparrow	G	—	0.5 ± 1.0	—	—	—
	S	—	0.2 ± 0.4	< 0.1	0.1 ± 0.3	—
	R	—	—	—	*	—

Table 6 continued.

Common name	Vegetation Type	Seasonal distribution and abundance 1975–1981				
		Number/Kilometer ± SD				
		February	April	June	August	October
Lark Sparrow	G	—	< 0.1	0.5 ± 0.5	0.2 ± 0.3	< 0.1
	S	—	< 0.1	1.2 ± 0.9	0.2 ± 0.3	—
	J	—	—	0.3 ± 0.3	*	< 0.1
	R	—	*	0.8 ± 0.7	0.5 ± 1.1	—
Black-throated Sparrow	G	—	0.4 ± 0.5	2.0 ± 0.7	1.3 ± 1.0	—
	S	—	0.1 ± 0.3	0.9 ± 0.5	0.2 ± 0.3	—
	J	—	0.1 ± 0.2	0.6 ± 0.6	0.3 ± 0.3	—
	R	—	—	< 0.1	< 0.1	—
Sage Sparrow	G	—	0.3 ± 0.4	0.2 ± 0.3	0.9 ± 1.8	0.6 ± 0.8
	S	*	2.5 ± 2.4	1.7 ± 1.3	1.0 ± 1.0	0.7 ± 0.8
	J	—	—	*	< 0.1	< 0.1
	R	—	< 0.1	—	< 0.1	0.2 ± 0.4
Song Sparrow	G	*	—	—	—	*
	R	< 0.1	*	*	—	< 0.1
White-crowned Sparrow	G	*	0.2 ± 0.4	*	—	0.2 ± 0.4
	S	—	*	*	—	—
	J	—	—	—	—	*
	R	0.2 ± 0.3	0.8 ± 1.1	< 0.1	—	2.2 ± 3.2
Dark-eyed Junco	G	—	3.0 ± 6.6	—	—	0.6 ± 0.9
	S	—	0.1 ± 0.3	—	—	< 0.1
	J	< 0.1	4.2 ± 6.8	*	—	0.9 ± 1.1
	R	6.8 ± 10.1	1.4 ± 1.4	—	—	5.8 ± 4.1
Red-winged Blackbird	G	—	*	*	*	—
	R	*	0.3 ± 0.8	< 0.1	—	*
Western Meadowlark	G	—	0.6 ± 0.9	0.8 ± 1.0	0.4 ± 0.4	< 0.1
	S	—	1.9 ± 0.6	1.8 ± 1.2	1.2 ± 1.1	1.1 ± 1.0
	J	—	*	< 0.1	—	—
	R	—	0.4 ± 0.3	0.2 ± 0.3	< 0.1	0.1 ± 0.3
Brewer's Blackbird	G	—	*	0.4 ± 0.9	—	—
	S	—	0.2 ± 0.4	< 0.1	*	—
	J	—	—	0.1 ± 0.3	—	—
	R	0.7 ± 1.7	< 0.1	< 0.1	—	0.6 ± 1.3
Brown-headed Cowbird	G	—	—	*	—	—
	S	—	*	*	—	—
	J	—	—	0.3 ± 0.3	—	—
	R	—	*	4.1 ± 1.6	0.3 ± 0.8	—
Northern Oriole	R	—	—	1.5 ± 1.0	0.1 ± 0.2	—
Scott's Oriole	G	—	—	< 0.1	< 0.1	—
	J	—	—	*	*	—
	R	—	—	—	*	—
Rosy Finch	G	1.5 ± 4.0	—	—	—	—
	S	0.1 ± 0.4	*	—	—	—
	J	1.7 ± 4.5	—	—	—	—
	R	4.8 ± 12.6	*	—	—	—
Northern Finch	G	*	0.3 ± 0.8	0.4 ± 0.4	< 0.1	0.2 ± 0.3
	S	—	0.1 ± 0.4	< 0.1	*	—
	J	—	1.3 ± 1.4	2.1 ± 1.0	0.8 ± 1.4	< 0.1
	R	0.5 ± 1.3	3.7 ± 3.5	6.0 ± 6.8	0.8 ± 0.8	4.8 ± 9.1
Pine Siskin	G	—	< 0.1	—	—	*
	S	—	*	—	—	—
	J	—	*	—	—	*
	R	< 0.1	*	—	—	< 0.1
American Goldfinch	G	—	—	—	*	—
	J	—	*	< 0.1	< 0.1	—
	R	0.2 ± 0.4	0.4 ± 1.2	0.4 ± 0.6	0.1 ± 0.2	—

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[1] Data from evening transects for 1977–1981

[2] Evacuation Creek exclusively

(*Haliaeetus leucocephalus*) was a consistent and numerous winter resident (26 in February 1984) along the White River, where it roosted and foraged. Foraging also occurred along Evacuation Creek and as far as 8 km (5 mi) north of the river in shadscale vegetation, where sheep provided the foraging eagles with carrion.

GALLIFORMES, GRUIFORMES, AND CHARADRIIFORMES.—Upland gamebirds, cranes, rails, and shorebirds constituted a minor portion of the avifauna of Ua-Ub (Table 5). The chukar (*Alectoris chukar*) was unsuccessfully planted by the Utah Division of Wildlife Resources (UDWR) in 1982 and 1983; earlier unsuccessful releases were reported by Olsen (1973). The sandhill crane (*Grus canadensis*) migrated over Ua-Ub in April and October. Flocks ranged from 15 to 300 individuals and migration usually lasted a minimum of two weeks. On 10 October 1976 a single whooping crane (*Grus americana*) accompanied a large flock of sandhill cranes. Sandhill cranes seldom roosted along the White River, preferring the Green River and adjacent agricultural fields near Jensen, Utah. Of the 36 species of shorebird recorded in the Uinta Basin, only 6 occurred along the White River. The most abundant and consistently present species was the spotted sandpiper (*Actitus macularia*) (Table 5).

COLUMBIFORMES.—The mourning dove (*Zenaida macroura*) was the only columbid encountered at Ua-Ub (Table 5). Doves preferred riparian habitat but nested in all habitats, slightly favoring juniper woodlands. Peak abundance occurred in 1975 and 1976, compared to 1977, 1979, and 1982 ($p \leq 0.05$), and the seasonal abundance peak was in August (Table 6).

CUCUCLIFORMES, STRIGIFORMES, AND CAPRIMULGIFORMES.—The yellow-billed cuckoo (*Coccyzus americanus*) was a new record for the Uinta Basin. It occurred in the tamarisk-cottonwood-rabbitbrush ecotone in riparian vegetation.

Of the four owls at Ua-Ub (Table 5), the great horned owl (*Bubo virginianus*) was the most abundant raptor, nesting in sandstone cavities both along the White River and in steep-walled dry washes associated with greasewood and juniper habitats. The long-eared owl (*Asio otus*) nested in cottonwoods and was encountered only from February through August. Data from another location in the Basin about 12 km (7 mi) south of the White River showed that long-eared owls roosted in isolated tamarisk and cottonwood trees and foraged in open shrublands from September through January (C. V. Grant, unpublished data). These owls apparently migrated into riparian woodlands to breed and returned to open shrublands to winter.

The common poor-will (*Phalaenoptilus nuttallii*) was more numerous than indicated by transect results (Table 5). It was encountered after sunset along roads throughout the upland habitats. The only transect encounter was an individual tending its scrape nest at the base of a juniper. The common nighthawk (*Chordeiles minor*) was more numerous than morning counts indicated; therefore, from 1977 through 1981 evening counts were used. Although nighthawks foraged throughout Ua-Ub, most nested in juniper woodlands. By August abundance remained the same in the uplands but increased decidedly in the riparian (Table 6) due to large flocks of foraging nighthawks.

APODIFORMES, CORACIIFORMES, AND PICIFORMES.—The white-throated swift (*Aeronautes saxatalis*) nested on the sandstone cliffs along the White River and foraged both in riparian and in adjacent upland habitats, especially shadscale (Table 5). During April swifts preferred to forage near the sandstone cliffs in the two wooded habitats.

The black-chinned hummingbird (*Archilochus alexandri*) concentrated in juniper and the broad-tailed hummingbird (*Selasphorus platycercus*) in riparian (Table 5). The belted kingfisher (*Ceryle alcyon*) was transient in April and October when river sediment was low.

Of the three resident woodpeckers, the northern flicker (*Colaptes auratus*) was the most abundant (Table 5). Most flickers moved to other locales during February, and occurred throughout Ua-Ub during April and October (Table 6). During June and August the population concentrated in riparian habitat.

PASSERIFORMES.—Included among nine species of flycatcher occurring at Ua-Ub was one new to the Uinta Basin, the eastern phoebe (*Sayornis phoebe*) (Table 5). Most flycatchers preferred riparian habitat except Say's phoebe (*Sayornis saya*) and the gray flycatcher (*Empidonax wrightii*). Say's phoebe occurred in riparian habitat during spring migration, but few nested along the river from 1975 to 1981 (Table 6). However, during June 1982 the phoebe population reached a 10-year peak (0.7 ± 0.5 birds/km) ($p \leq 0.05$), as indicated by a distinct increase in abundance of the bird in shadscale (0.6 birds/km) and riparian (1.4 birds/km) habitats. By June 1984 no phoebes occurred in riparian but were still abundant in shadscale. The gray flycatcher preferred juniper habitat and foraged in adjacent greasewood and, like most flycatchers except Say's phoebe, left Ua-Ub by August (Table 6).

The horned lark (*Eremophilus alpestris*), a permanent resident of Ua-Ub, was most abundant during winter (Table 6). Breeding and nesting abundance was consistently low. It preferred a flatter terrain of low desert shrubs found west of Ua-Ub for nesting. Near Cottonwood Wash, southeast of Ouray, Utah, during June 1982 horned larks nested at the rate of 10 birds per transect kilometer in both shadscale and matted saltbush habitats type (C. V. Grant, unpublished data).

Swallows were abundant. The violet-green swallow (*Tachycineta thalassina*) nested in sandstone in juniper woodlands and foraged in greasewood draws. The cliff swallow (*Hirundo pyrrhonota*) was the most abundant bird at Ua-Ub (Table 5). Cliff swallows built mud nests on sandstone cliffs along the White River, especially during 1982 and 1983 (70 and 99 swallows per transect kilometer, respectively).

Two abundant corvids were the black-billed magpie (*Pica pica*) and pinyon jay (*Gymnorhinus cyanocephalus*) (Table 5). Magpies preferred riparian habitat but did nest in juniper woodlands. Jays nested and foraged in juniper, foraged in greasewood, avoided riparian, and used shadscale only in late summer (Table 6). Magpie populations reached peak abundance in 1978 (1.6 birds per transect kilometer) ($p \leq 0.05$). The peak was preceded by high abundance from 1975 through 1977 and followed by a decline from 1979 through 1984. Pinyon jay populations peaked in 1982 (9.9 birds per transect kilometer; $p \leq 0.05$), exceeding all other years except 1978.

The black-capped chickadee (*Parus atricapillus*) was a consistent resident in riparian, and the plain titmouse (*P. inornatus*) was a consistent resident in juniper (Table 5). The titmouse was found in juniper throughout the year, whereas the chickadee moved into the uplands in October and February just as the mountain chickadee (*P. gambeli*) moved to lower elevations at Ua-Ub (Table 6).

The most abundant and ubiquitous of the five wrens was the rock wren (*Salpinctes obsoletus*) (Table 5). Its presence in riparian was limited to areas of sandstone outcropping and greasewood along the riparian edge. Unlike many birds at Ua-Ub, including the house wren (*Troglodytes aedon*) and Bewick's wren (*Thryomanes bewickii*), the rock wren population did not disperse by August (Table 6).

The American robin (*Turdus migratorius*) was limited in distribution to riparian habitat (Table 5) from June through October but occurred in greasewood and juniper habitats during spring migration (Table 6). The mountain bluebird (*Sialia curricoides*), known to migrate through the Basin lowlands but nest above 8,000 ft (Behle 1981), also nested in low-elevation juniper and riparian woodlands and foraged in adjacent shrublands (Table 5). Although about 50% of the breeding bluebirds dispersed by August, they congregated at Ua-Ub during fall migration at a higher but more variable abundance (Table 6).

The most unexpected bird to occur at Ua-Ub was the black-tailed gnatcatcher (*Polioptila melanura*). Behle and Perry (1975) and Hayward et al. (1976) considered this species unconfirmed in the southwestern corner of Utah. Its occurrence in the northeastern corner of the state would have to be discounted except for the numerous individuals identified during 1975 (Tables 5 and 6) and the interactions with the blue-gray gnatcatcher (*P. caerulea*) in riparian habitats.

Among the mimids, the northern mockingbird (*Mimus polyglottus*) was a sporadic resident in greasewood and the sage thrasher (*Oreoscoptes montanus*) a consistent summer resident in shadscale (Table 5). Two rare mimids were Bendire's thrasher (*Toxostoma bendirei*), identified by David M. Smith (USFWS, Washington, D.C., personal communication) in June 1976, a species new to the Basin, and the gray catbird (*Dumetella caroli-*

nensis), identified by S. B. Vander Wall in June 1982. Another Bendire's thrasher, a singing male, was observed in greasewood habitat in Cottonwood Wash, west of Ua-Ub in June 1982 (C. V. Grant, unpublished data).

All birds with abundance exceeding one bird per kilometer were present in more than one season except the cedar waxwing (*Bombycilla cedrorum*) (Table 5). Abundance was high and nesting apparently took place among the cottonwoods during June, but no waxwings occurred at Ua-Ub at any other time.

Of the four vireos occurring at Ua-Ub, the gray vireo (*Vireo vicinior*), also identified by Vander Wall, was new to the Uinta Basin, and the red-eyed vireo (*V. olivaceus*) was recorded only once before by Twomey (1942).

One new species of Emberizidae was recorded for the Basin, the rose-breasted grosbeak (*Pheuticus ludovicianus*). One individual was recorded in juniper in June 1976, and what appeared to be two breeding pairs were sighted in riparian in June 1983.

Most warblers occurred in riparian woodlands (Table 5), specifically the yellow warbler (*Dendroica petechia*) in cottonwoods and the yellow-breasted chat (*Icteria virens*) in tamarisks. The black-throated gray warbler (*Dendroica nigrescens*) was the only parulid in juniper woodlands. Some individuals moved into riparian habitat during August (Table 6).

Other abundant summer residents in riparian were the western tanager (*Piranga ludoviciana*), lazuli bunting (*Passerina amoena*), and rufous-sided towhee (*Pipilo erythrophthalmus*). Among the sparrows, the American tree sparrow (*Spizella arborea*) was an abundant winter resident but occurred only in the mixture of tamarisk and greasewood along Evacuation Creek.

Among the summer residents, the chipping sparrow (*Spizella passerina*) favored juniper woodlands, the Brewer's (*S. breweri*) and black-throated sparrow (*Amphispiza bilineata*) favored greasewood, and the lark (*Chondestes grammacus*) and sage sparrow (*Amphispiza belli*) favored shadscale (Table 5). Most of the sparrows remained at Ua-Ub through August, with sage sparrows the earliest to arrive and the last to leave (Table 6).

Chipping sparrows were at peak abundance in 1975 compared to 1976–1984 ($p \leq 0.05$). Brewer's sparrows also peaked in 1975 compared to 1976–1981 ($P \leq 0.05$). Lark sparrows peaked in 1976 and 1981 compared to 1977–1980 and 1983–1984 ($p \leq 0.05$). Neither of the desert sparrow populations, the black-throated and sage, changed significantly from year to year.

Among the icterids, the western meadowlark (*Sturnella neglecta*) preferred desert shrub over wooded habitats and shadscale over all habitats (Table 5). Both the brown-headed cowbird (*Molothrus ater*) and the northern oriole (*Icterus galbula*) were abundant residents of riparian woodlands. The former was also present in juniper during years of high black-throated gray warbler abundance. Scott's oriole (*Icterus parisorum*), classified as a rare summer resident of the Uinta Basin (Behle 1981), was few but consistent at Ua-Ub from 1975 through 1981. Individuals or a nesting pair were seen at least once at one location during any one year. Abundance increased from 1982 through 1984, when at least two pairs nested in greasewood-juniper uplands and were encountered on a daily rather than annual basis.

Two abundant fringillids were the rosy finch (*Leucosticte arctoa*), a winter resident dominated by the black subspecies (*L. a. atrata*), and the northern finch (*Carpodacus mexicanus*), more often summer residents (Table 5) but occasionally present year-round in its preferred riparian habitat (Table 6). The latter nested in both wooded habitats.

Mammalia

CHIROPTERA.—Nine species of bats, plus what may be four additional species, occurred at Ua-Ub (Table 7). Difficulty in species recognition due to possible species integration (Parkinson 1979) led to combining the little brown bat (*Myotis lucifugus*) and Yuma bat (*M. yumanensis*). Although some easily recognizable characteristics may distinguish the California bat (*M. californicus*) from the small-footed bat (*M. leibii*), we could not find one that was consistent, a problem also noted by Bogan (1974). Two new species for the Basin, both expected but never captured (Durrant 1952), were the long-legged bat (*M. volans*) and hoary bat (*Lasiurus cinereus*). Hasenyager (1980) included a record for the former species for Duchesne County but did

TABLE 7. Mammalian residency status, consistency, spatial distribution, and abundance in four vegetation types at Oil Shale Tracts Ua-Ub. Abbreviations are explained in Table 1. Letters after abundance indicate differences at $p \leq 0.05$.

ORDER **Family** Common name *Genus species*	Spatial distribution and abundance 1975–1984				
	Residency status	Years present	Month	Vegetation type	Individuals/ trap night ± SD
CHIROPTERA					
Vespertilionidae					
Little Brown/Yuma Bat	?	3	June	Gp	0.6 ± 1.4
Myotis lucifugus/M. yumanensis			August	Gp	0.3 ± 0.7
Long-eared Bat	S	4	June	Gp	0.4 ± 0.5
Myotis evotis			August	Gp	0.4 ± 0.6
Long-legged Bat	S	4	June	Gp	1.4 ± 1.9
Myotis volans			August	Gp	1.1 ± 1.8
California/Small-footed Bat	?	4	June	Gp	2.0 ± 2.0 a
Myotis californicus/ M. leibii			August	Gp	0.6 ± 1.0 b
Silver-haired Bat	m	4	June	Gp	2.0 ± 2.4 a
Lasionycteris noctivagans			August	Gp	0.2 ± 0.4 b
Western Pipistrelle	P	4	June	Gp	2.9 ± 2.6
Pipistrellus hesperus			August	Gp	4.7 ± 5.2
Big Brown Bat	?	1	June	Gp	0.05
Eptesicus fuscus					
Hoary Bat	S	4	June	Gp	8.1 ± 6.9 a
Lasiurus cinereus			August	Gp	3.5 ± 3.8 b
Townsend's Big-eared Bat	?	1	August	Gp	0.05
Plecotus townsendii					
Pallid Bat	S	4	June	Gp	0.6 ± 0.9
Antrozous pallidus			August	Gp	0.5 ± 1.0
Molassidae					
Brazilian Free-tailed Bat	?	1	June	Gp	0.05
Tadarida brasiliensis					
					Number/ kilometer ± SD
LAGOMORPHA					
Lepidae					
Desert Cottontail	P	10	August	G	2.6 ± 2.9
Sylvilagus audubonii				S	2.0 ± 2.0
				J	2.1 ± 2.4
				R	2.2 ± 3.4
Black-tailed Jackrabbit	P	6	August	G	*
Lepus californicus				S	*
				J	0.06
					Ind/ha ± SD (no/km ± SD)
RODENTIA					
Sciuridae					
Least Chipmunk	P	10	August	G	0.1 ± 0.2 a
Eutamias minimus				S	*
				J	1.4 ± 1.4 b
				R	0.1 ± 0.3 a
Colorado Chipmunk	?	1	June	J	*
Eutamias quadrivittatus					

Table 7 continued.

ORDER	Spatial distribution and abundance 1975–1984				
Family Common name *Genus species*	Residency status	Years present	Month	Vegetation type	Individuals/ trap night ± SD
Yellow-bellied Marmot	P	6	August	G	*
Marmota flaviventris				S	*
				R	*
White-tailed Antelope Squirrel	P	10	August	G	1.4 ± 2.1
Ammospermophilus leucurus				S	1.1 ± 1.9
				J	0.4 ± 0.5
				R	*
Rock Squirrel	P	3	August	G	*
Spermophilus variegatus				S	*
				R	*
Golden-mantled Ground Squirrel	P	10	August	G	(0.04)
Spermophilus lateralis				S	(0.01)
				J	(0.06)
				R	(0.08)
White-tailed Prairie Dog	P	7	August	G	*
Cynomys leucurus				S	*
Heteromyidae					
Apache Pocket Mouse	P	10	August	G	2.6 ± 2.2 a
Perognathus apache				S	2.6 ± 1.4 a
				J	1.3 ± 0.9 b
				R	0.08 b
Ord's Kangaroo Rat	P	10	August	G	7.3 ± 5.7 a
Dipodomys ordii				S	3.3 ± 2.4 b
				J	0.2 ± 0.4 c
				R	0.9 ± 1.4 c
Castoridae					
Beaver	P	10	August	G	*
Castor canadensis				S	*
				R	(0.1 ± 0.2)
Cricetidae					
Western Harvest Mouse	P	10	August	G	0.6 ± 0.7 a
Reithrondontomys megalotis				S	1.2 ± 2.1
				J	0.1 ± 0.2 a
				R	1.8 ± 2.1 b
Canyon Mouse	P	9	August	S	*
Peromyscus crinitus				J	1.0 ± 1.0
				R	*
Deer Mouse	P	10	August	G	5.8 ± 5.7 a
Peromyscus maniculatus				S	6.0 ± 6.2 a
				J	4.2 ± 2.6 a
				R	16.9 ± 10.9 b
Brush Mouse	P	4	August	S	0.06
Peromyscus boylii				R	0.1 ± 0.3
Pinyon Mouse	P	8	August	G	0.2 ± 0.2
Peromyscus truei				S	*
				J	1.4 ± 1.9
				R	*
Desert Woodrat	P	10	August	G	0.3 ± 0.6 a
Neotoma lepida				S	0.2 ± 0.6 a
				J	2.7 ± 2.6 b
				R	0.1 ± 0.3 a

Table 7 continued.

ORDER **Family** Common name *Genus species*	Spatial distribution and abundance 1975–1984				
	Residency status	Years present	Month	Vegetation type	Individuals/ trap night ± SD
Bushy-tailed Woodrat	P	10	August	G	*
Neotoma cinerea				S	*
				J	0.7 ± 1.0
				R	1.4 ± 2.0
Montane Vole	P	4	August	G	*
Microtus montanus				S	0.1 ± 0.3
				R	3.5 ± 7.6
Muskrat	P	10	August	R	*
Ondatra zibethicus					
Erethizontidae					
Porcupine	P	10	August	G	*
Erethizon dorsatum				J	*
				R	(0.02)
					Number/ Kilometer ± SD
CARNIVORA					
Canidae					
Coyote	P	10	August	G	*
Canis latrans				S	*
				J	*
				R	*
Red Fox	?	1	August	S	*
Vulpes vulpes					
Gray Fox	?	1	October	R	*
Urocyon cinereoargenteus					
Procyonidae					
Ringtail	?	1	April	J	*
Bassariscus astutus					
Raccoon	P	7	August	R	*
Procyon lotor					
Mustelidae					
Long-tailed Weasel	t	2	June	J	*
Mustela frenata					
Badger	P	9	August	G	*
Taxidea taxus				S	*
				J	*
				R	*
Striped Skunk	P	9	August	R	0.01
Mephistis mephistis					
Felidae					
Mountain Lion	t	1	June	S	*
Felis concolor					
Bobcat	P	4	August	G	*
Lynx rufus				S	*
				J	*
				R	*
ARTIODACTYLA					
Cervidae					
Mule Deer	P	10	August	G	0.05
Odocoileus hemionus				S	0.1 ± 0.2
				J	0.1 ± 0.2
				R	0.4 ± 0.3

Table 7 continued.

ORDER Family Common name *Genus species*	Spatial distribution and abundance 1975–1984 Residency status	 Years present	 Month	 Vegetation type	 Individuals/ trap night ± SD
Antilocapridae					
Pronghorn	t	2	August	S	*
Antilocapra americana				R	*
Bovidae					
Bighorn Sheep	t	1	April	S	*
Ovis canadensis					
Domestic Sheep	w	10	February	G	13.5 ± 22.9
Ovis aries				S	*
				J	15.8 ± 40.7
				R	15.0 ± 24.7
Domestic Cattle	S	10	August	G	*
Bos taurus				S	0.06
				R	4.5 ± 3.9

not cite the record. The fringed bat (*M. thysanodes*) was also recorded for the Basin with no source in Hasenyager (1980), and the only other record was Krutszch and Heppenstall (1955) from the Book Cliffs at the southern boundary of the Basin.

One of the most abundant bats was the western pipistrelle (*Pipistrellus hesperus*), the smallest bat at Ua-Ub, weighing 4 ± 0.4 g. It was a permanent resident that was encountered in all seasons and was the only species to increase in abundance during August. During the 1977 drought the western pipistrelle and the silver-haired bat (*Lasionycteris noctivagans*) were the only species to occur in high abundance.

Silver-haired bats, weighing 10 ± 1 g, were migrants. Usually the June population was predominantly male; however, females accompanied the males during 1978 and 1980. During August, only three males were captured in four years. This bat, like the hoary bat, migrates northward in segregated groups, pregnant females preceding the males (Barbour and Davis 1969).

The largest and most abundant species was the hoary bat, females being larger than males, 26 ± 3 g and 24 ± 3 g, respectively ($p \leq 0.05$), and pregnant females the largest at 34 ± 3 g ($p. \leq 0.05$). During June the population was usually dominated by males (97%) from 1977 to 1979. During August 1977–1979 the sex ratio was even (49% male). During June 1980 the ratio changed to 65% male. All 13 females trapped during June 1980 were pregnant. During August 1980 the ratio increased to 86% male, 50% of these subadults. Only three females were observed. None displayed the usual signs of copulation.

Pregnant females were thought to occur in the plains for parturition, join the males in the Intermountain West in late summer, and breed at some unknown time in the fall prior to migrating into the southwestern states and northern Mexico for the winter (Findley and Jones 1964). At Ua-Ub breeding occurred in August as noted by Merriam (1884) and Tenaza (1966); males and females were not segregated during parturition, which in 1980 occurred in the Intermountain West.

LAGOMORPHA.—Only two species of lagomorph occurred at Ua-Ub, the desert cottontail (*Sylvilagus audubonii*) and black-tailed jackrabbit (*Lepus californicus*) (Table 7). The white-tailed jackrabbit (*L. townsendii*) occurred near Bonanza, Utah, but sightings were rare over a 10-year period. Cottontails were the most numerous mammal encountered on transects. Although no habitat preference was evident, annual changes reflected the cyclic nature of lagomorph populations (Fig. 8). Abundance during 1976 and 1983 exceeded all other years ($p \leq 0.01$), and 1977–1978 and 1982 exceeded abundance during 1979–1981 and 1984 ($p \leq 0.05$). The rapid increase in 1976 following a 1975 desert bloom kept the cottontail population at a high level through the 1977 drought. The severe

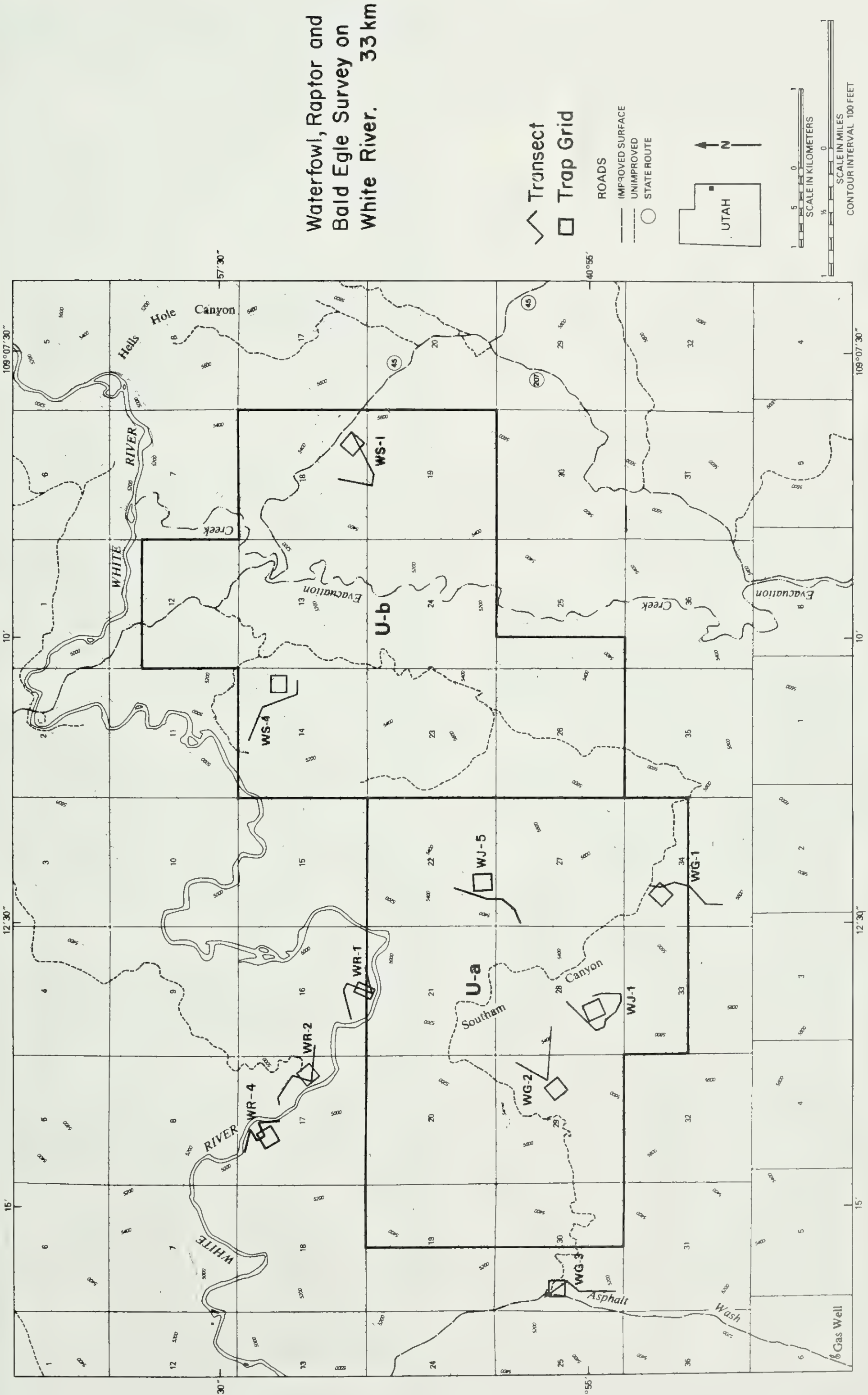
Waterfowl, Raptor and Bald Egle Survey on White River. 33 km
Transect
Trap Grid
ROADS
IMPROVED SURFACE
UNIMPROVED
STATE ROUTE
UTAH
N
SCALE IN KILOMETERS
SCALE IN MILES
CONTOUR INTERVAL 100 FEET
109°07'30"
10'
12'30"
15'
57'30"
40°55'
U-a
U-b
WS-1
WS-4
WJ-1
WJ-5
WG-1
WG-2
WG-3
WR-1
WR-2
WR-4
WHITE RIVER
Hells Hole Canyon
Evacuation Creek
Southam Canyon
Asphalt Wash
Gas Well
45
207

Fig. 7. Wildlife sampling locations at Oil Shale Tracts Ua-Ub, Uintah County, Utah. WG–greasewood sites; WS–shadscale sites; WJ–juniper sites; WR–riparian sites.

Table 7 continued.

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Bighorn Sheep	t	1	April	S	*
Ovis canadensis					
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				R	4.5 ± 3.9

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Pregnant females were thought to occur in the plains for parturition, join the males in the Intermountain West in late summer, and breed at some unknown time in the fall prior to migrating into the southwestern states and northern Mexico for the winter (Findley and Jones 1964). At Ua-Ub breeding occurred in August as noted by Merriam (1884) and Tenaza (1966); males and females were not segregated during parturition, which in 1980 occurred in the Intermountain West.

LAGOMORPHA.—Only two species of lagomorph occurred at Ua-Ub, the desert cottontail (*Sylvilagus audubonii*) and black-tailed jackrabbit (*Lepus californicus*) (Table 7). The white-tailed jackrabbit (*L. townsendii*) occurred near Bonanza, Utah, but sightings were rare over a 10-year period. Cottontails were the most numerous mammal encountered on transects. Although no habitat preference was evident, annual changes reflected the cyclic nature of lagomorph populations (Fig. 8). Abundance during 1976 and 1983 exceeded all other years ($p \leq 0.01$), and 1977–1978 and 1982 exceeded abundance during 1979–1981 and 1984 ($p \leq 0.05$). The rapid increase in 1976 following a 1975 desert bloom kept the cottontail population at a high level through the 1977 drought. The severe

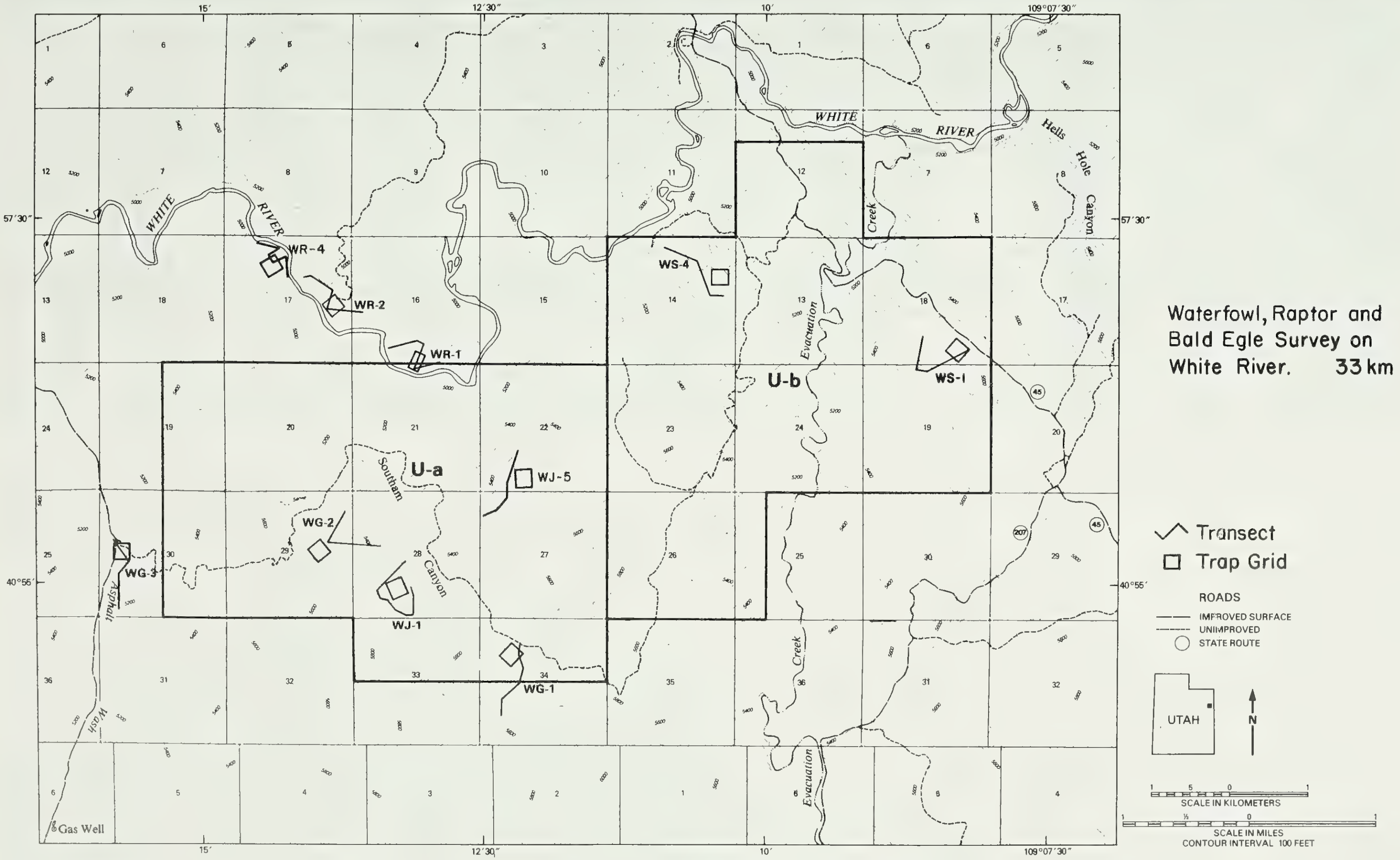
Waterfowl, Raptor and
Bald Egle Survey on
White River. 33 km
Transect
Trap Grid
ROADS
IMPROVED SURFACE
UNIMPROVED
STATE ROUTE
UTAH
N
SCALE IN KILOMETERS
SCALE IN MILES
CONTOUR INTERVAL 100 FEET
U-a
U-b
WR-1
WR-2
WR-4
WS-1
WS-4
WJ-1
WJ-5
WG-1
WG-2
WG-3
WHITE RIVER
Hells Hole Canyon
Evacuation Creek
Southam Canyon
Asphalt Wash
Gas Well
15′
12′30″
10′
109°07′30″
57′30″
40°56′
40°55′

Fig. 7. Wildlife sampling locations at Oil Shale Tracts Ua-Ub, Uintah County, Utah. WG–greasewood sites; WS–shadscale sites, WJ–juniper sites; WR–riparian sites.

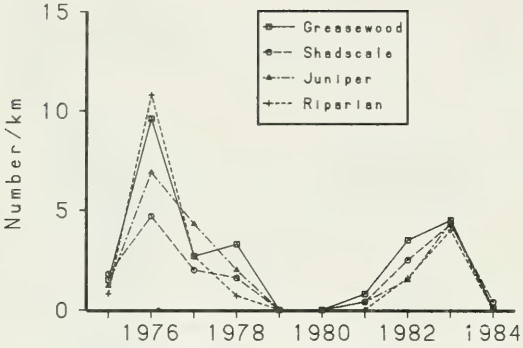

Fig. 8. Desert cottontail (*Sylvilagus audubonii*) abundance in four vegetation types at Oil Shale Tracts Ua-Ub, Uintah County, Utah.

winter of 1978–1979 resulted in small pockets of surviving cottontails in juniper and riparian woodlands and extinction in shrub habitats from 1979 through 1980. The crash in 1984 also followed a severe winter. Seasonally, cottontails were at peak abundance during August and October ($p \leq 0.05$) (Table 8).

RODENTIA.—Twenty species of rodents occurred at Ua-Ub (Table 7). In the squirrel family, the least chipmunk (*Eutamias minimus*) favored juniper habitat. It was seldom seen or captured in February and was most active during June and August (Table 8). It avoided shadscale habitats that lacked scattered juniper trees and plentiful sandstone outcrops. The Colorado chipmunk (*E. quadrivittatus*) was a rare capture in juniper (Table 8), though Ranck (1961) found them relatively common in similar habitat.

The yellow-bellied marmot (*Marmota flaventris*) was rare until 1981, when encounters became frequent in the rip-rap used to construct a bridge and pipeline across the White River.

The white-tailed antelope squirrel (*Ammospermophilus leucurus*) densities in greasewood and shadscale were five and four per hectare, respectively, and one per hectare in juniper from 1975 through 1976, exceeding the next eight years ($p \leq 0.05$). During the 1977 drought through 1980 no squirrels were captured or seen in shadscale and juniper habitats. Visual sighting during the day occurred in February in greasewood, then from April through October after sunset or prior to dawn. The squirrel population appeared to be recovering in 1982; however, density declined to 0.1 per hectare in 1984.

The white-tailed prairie dog (*Cynomys leucurus*) that resided in a town on the northeastern perimeter of Ub followed the same pattern as the antelope squirrel. The dog town was abandoned from 1977 through 1980, was recolonized by individuals from larger towns to the north in 1981, then "boomed" in 1984.

Two heteromyid rodents, the Apache pocket mouse (*Perognathus apache*) and Ord's kangaroo rat (*Dipodomys ordii*), favored greasewood and shadscale habitats (Table 7). Pocket mice were especially susceptible to cold weather, with no captures occurring in February, whereas kangaroos rats remained active through mild winters (Table 8). Annually pocket mice were little affected by drought or the 1975 bloom; however, the severe winter of 1979 may have influenced the population to a small degree.

Ord's kangaroo rats were not affected by the drought, but following 1979 the population began to increase, reaching a peak in 1980 and 1981 ($p \leq 0.05$) (Fig. 9). Kangaroo rats invaded riparian and juniper habitats, occupying sandy fluvial deposits and sandy alluvial deposits from upland flashfloods in riparian habitat and sandy alluvial and colluvial deposits in the juniper. By 1984 these populations were extinct and the normally stable populations in shrub habitats were also declining.

The beaver (*Castor canadensis*), absent from the White River in previous surveys (Ranck 1961, Olsen 1973), resided in the river banks and was active year-round, even during winters when the river was frozen over. Young beaver was encountered in shadscale and in ponds in Asphalt Wash during August.

The cricetid rodents were species of the woodlands rather than the shrubs. The western harvest mouse (*Reithrodontomys megalotis*) and deer mouse (*Peromyscus maniculatus*) preferred riparian woodlands, and the canyon mouse (*P. crinitus*), pinyon mouse (*P. truei*), and desert woodrat (*Neotoma lepida*) preferred juniper (Table 7). The bushytailed woodrat (*N. cinerea*) preferred both woodlands, and it, like the desert woodrat, was subject to periodic extinction in greasewood and shadscale.

All these rodents were active year-round (Table 8). Annually two basic patterns in population were demonstrated by the harvest mice (Fig. 10) and by the deer mice (Fig. 11). The harvest mice were present some years and absent others, as were the canyon mice, the pinyon mice, the least chipmunks, and the montane

Table 8. Mammalian seasonal distribution and abundance in four vegetation types at Oil Shale Tracts Ua-Ub. Abbreviations are explained in Table 1.

		Seasonal distribution and abundance 1975–1981				
		Individuals/100 trap nights ± SD (Number/Kilometer ± SD)				
Species	Vegetation type	February	April	June	August	October
Desert Cottontail	G	(2.0 ± 2.8)	(0.6 ± 0.8)	(2.7 ± 3.2)	(2.6 ± 3.4)	(3.4 ± 5.9)
	S	(0.9 ± 0.9)	(0.6 ± 0.8)	(1.2 ± 1.3)	(1.5 ± 1.6)	(1.2 ± 2.2)
	J	(0.6 ± 0.8)	(0.7 ± 1.2)	(0.8 ± 0.8)	(2.1 ± 2.6)	(2.0 ± 2.7)
	R	(0.3 ± 0.4)	(1.2 ± 1.6)	(1.5 ± 1.8)	(2.1 ± 3.9)	(2.9 ± 4.1)
Least Chipmunk	G	—	*	*	0.1 ± 0.3	< 0.1
	S	—	0.3 ± 0.8	0.1 ± 0.3	0.2 ± 0.5	—
	J	*	0.7 ± 1.2	1.8 ± 1.1	1.9 ± 2.2	1.2 ± 1.4
	R	—	—	*	—	—
Colorado Chipmunk	J	—	0.1 ± 0.3	< 0.1	—	—
White-tailed Antelope Squirrel	G	*	*	0.2 ± 0.6	0.6 ± 0.9	0.4 ± 0.7
	S	0.2 ± 0.4	*	0.2 ± 0.3	0.1 ± 0.4	0.1 ± 0.3
	J	*	*	0.2 ± 0.5	0.1 ± 0.4	*
	R	—	—	*[1]	*[1]	—
Golden-mantled Ground Squirrel	G	(< 0.1)	*	(<0.1)	(<0.1)	*
	S	*	—	*	*	*
	J	*	*	(<0.1)	*	*
	R	—	*	(<0.1)	(0.1 ± 0.3)	*
Apache Pocket Mouse	G	—	1.1 ± 1.0	2.1 ± 1.9	2.0 ± 1.3	1.6 ± 1.0
	S	—	1.5 ± 1.5	2.0 ± 1.5	1.9 ± 1.5	0.9 ± 1.5
	J	—	0.6 ± 0.7	1.6 ± 1.3	1.4 ± 1.5	0.2 ± 0.4
	R	—	—	0.1 ± 0.4[1]	0.1 ± 0.3[1]	0.1 ± 0.3[1]
Ord's Kangaroo Rat	G	3.5 ± 4.2	6.0 ± 5.0	6.8 ± 6.2	7.4 ± 8.5	9.4 ± 9.5
	S	1.9 ± 2.1	1.4 ± 1.0	3.2 ± 3.4	2.4 ± 2.2	2.5 ± 2.0
	J	—	—	0.5 ± 1.3	0.4 ± 0.9	0.4 ± 0.8
	R	0.2 ± 0.4	—	0.5 ± 1.1	0.8 ± 1.5	0.5 ± 0.8
Beaver	R	(0.2 ± 0.3)	(< 0.1)	(0.3 ± 0.4)	(0.2 ± 0.3)	(< 0.1)
Western Harvest Mouse	G	1.3 ± 1.4	0.6 ± 1.3	0.5 ± 0.7	0.5 ± 1.1	0.3 ± 0.6
	S	0.3 ± 0.7	0.2 ± 0.4	—	0.2 ± 0.3	0.4 ± 0.4
	J	0.2 ± 0.4	0.2 ± 0.6	—	< 0.1	—
	R	—	1.1 ± 2.4	0.4 ± 1.0	0.9 ± 1.2	0.9 ± 1.2
Canyon Mouse	S	—	0.1 ± 0.3	0.2 ± 0.3	0.1 ± 0.3	—
	J	0.3 ± 0.4	0.6 ± 0.9	2.5 ± 2.4	2.0 ± 1.5	1.4 ± 1.9
	R	—	—	—	0.1 ± 0.4	—
Deer Mouse	G	4.8 ± 4.7	9.4 ± 6.3	5.3 ± 3.6	4.9 ± 5.9	12.1 ± 10.3
	S	8.6 ± 9.0	12.0 ± 12.4	9.4 ± 5.9	8.9 ± 6.4	13.1 ± 8.4
	J	4.8 ± 6.0	6.1 ± 6.0	6.3 ± 3.9	5.0 ± 4.8	9.2 ± 6.3
	R	7.7 ± 8.6	7.8 ± 4.1	11.4 ± 8.1	13.8 ± 10.4	14.2 ± 7.9
Pinyon Mouse	G	—	—	—	—	< 0.1
	J	0.6 ± 1.0	0.4 ± 1.1	0.9 ± 1.4	1.4 ± 2.1	2.7 ± 2.7
	R	0.2 ± 0.4	—	—	—	0.1 ± 0.3
Desert Woodrat	G	0.2 ± 0.4	< 0.1	0.3 ± 0.7	0.3 ± 0.7	< 0.1
	S	—	—	0.2 ± 0.5	0.5 ± 0.8	—
	J	0.5 ± 0.7	0.8 ± 1.3	1.5 ± 1.5	2.0 ± 2.3	2.8 ± 2.9
	R	—	—	0.1 ± 0.4	< 0.1	0.1 ± 0.3
Bushy-tailed Woodrat	G	—	0.5 ± 1.0	—	0.2 ± 0.5	0.4 ± 0.8
	S	0.2 ± 0.4	—	< 0.1	—	—
	J	0.5 ± 1.1	0.3 ± 0.6	0.2 ± 0.3	0.3 ± 0.4	1.1 ± 1.5
	R	—	—	0.1 ± 0.3	0.2 ± 0.4	0.1 ± 0.3

Table 8 continued.

		Seasonal distribution and abundance 1975–1981				
		Individuals/100 trap nights ± SD (Number/Kilometer ± SD)				
Species	Vegetation type	February	April	June	August	October
Porcupine	J	—	—	—	*	*
	R	(0.8 ± 0.6)	(0.4 ± 0.4)	(< 0.1)	(< 0.1)	(< 0.1)
Mule Deer	G	(< 0.1)	—	—	(< 0.1)	—
	S	(< 0.1)	(0.2 ± 0.3)	(< 0.1)	(< 0.1)	—
	J	(0.1 ± 0.2)	(< 0.1)	(< 0.1)	(< 0.1)	—
	R	—	(0.1 ± 0.3)	(0.1 ± 0.1)	(0.5 ± 0.3)	(0.7 ± 0.7)
Domestic Sheep	G	(13.5 ± 22.9)	*	—	—	—
	S	*	(54.3 ± 76.6)	*	—	—
	J	(15.8 ± 40.7)	*	—	—	—
	R	(15.0 ± 24.7)	*	*	*	*
Domestic Cattle	R	*	*	*	(6.1 ± 3.6)	(8.0 ± 8.8)

[1] Evacuation Creek exclusively

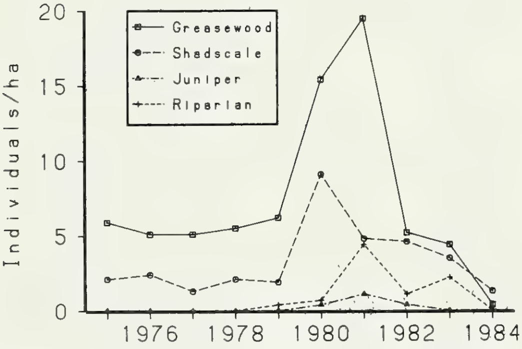

Fig. 9. Ord's kangaroo rat (*Dipodomys ordii*) density in four vegetation types at Oil Shale Tracts Ua-Ub, Uintah County, Utah.

voles (*Microtus montanus*). The pinyon mice seemed more like an invader from southerly pinyon-juniper woodlands during years of overall high rodent productivity.

Both types of woodrats followed the same pattern as the deer mice: high density in 1976, a crash in 1977, and a slow recovery and median densities in upland habitats. Deer mouse density in riparian habitat was possibly skewed upward by movement from shadscale into riparian habitats. The reasons for this movement were possibly wet soils in riparian, plus a lack of aboveground nest sites. In northwestern Colorado the deer mice moved more than 1 km in one week between dry soils covered by grasses and willow-dominated riparian vegetation (C. V. Grant, unpublished data).

Three other rodents of note were the montane vole, the muskrat (*Ondatra zibethicus*), and the porcupine (*Erethizon dorsatum*). The vole was new for this portion of the Uinta Basin (Durrant 1952). In 1981 the first vole was trapped along the White River. By 1982 vole density was 22 individuals per hectare on one alluvial fan, but no sign was present elsewhere along the river. By 1983 voles were present or trapped on every alluvial fan we visited, plus individuals were seen in greasewood habitat, 4 km south of the river in the Southam Canyon. By 1984 there were no signs nor captures of voles along the White River, but some were captured and more observed in shadscale habitat, 3 km south of the White River and 2 km east of Evacuation Creek at sampling site S1 (See Fig. 7).

Muskrats, previously unrecorded in these reaches of the White River, were not numerous but consistent. Porcupines were also few in number during summer (Table 7); peak abundance occurred during winter (Table 8) when they fed on the upper cottonwood canopy.

CARNIVORA.—Ten species of carnivore occurred at Ua-Ub (Table 7). The striped skunk, (*Mephistis mephistis*), coyote (*Canis latrans*), raccoon (*Procyon lotor*), and badger (*Taxidea taxus*) were the only consistent carnivores at Ua-Ub. None were abundant; only one striped skunk was encountered on transect. In areas where the prey base was more stable, carnivores were not only encountered on transects, but weasels (*Mustela* spp.) were captured in live traps (C. V. Grant, unpublished data).

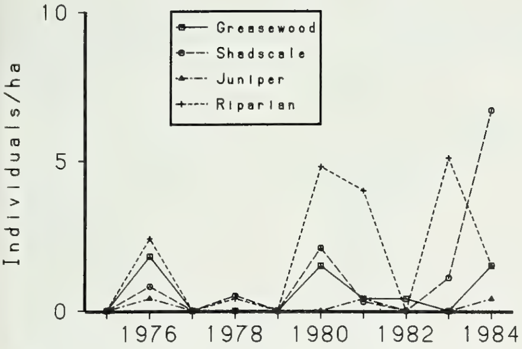

Fig. 10. Western harvest mouse (*Reithrodontomys megalotis*) density in four vegetation types at Oil Shale Tracts Ua-Ub, Uintah County, Utah.

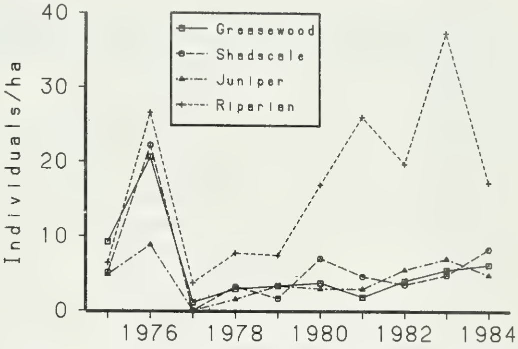

Fig. 11. Deer mouse (*Peromyscus maniculatus*) density in four vegetation types at Oil Shale Tracts Ua-Ub, Uintah County, Utah.

ARTIODACTYLA.—Mule deer (*Odocoileus hemionus*) occurred at low abundance at Ua-Ub (Table 7). They used both the juniper and shadscale during winter and early spring, then most deer moved into riparian for the remainder of the year. Pronghorn (*Antilocapra americana*) entered the boundary of Ua-Ub north of the White River on only two occasions, once during the 1977 drought and again in 1983. Bighorn sheep (*Ovis canadensis*) were encountered in high sandstone cliffs separating Asphalt Wash and Southam Canyon in April 1983. In June 1983 a group of three ewes was seen in high sandstone cliffs north of the White River at Ignatio Stage Stop. These sightings are the only living sheep reported in the Basin.

Two other mammals that are seldom considered in wildlife accounts yet play a major role in forage quantity and quality were domestic livestock. Domestic sheep (*Ovis aries*) were winter residents of Ua-Ub from December through April (Table 7). One flock of about 2,000 wintered in and around greasewood, juniper, and riparian habitats of Ua. This flock moved north of the White River in March, but at least two other flocks moved into Ub shadscale habitat from March through shearing in late April (Table 8).

Approximately 400 cattle were released in riparian habitat in late June to forage along the river bottom lands through October (Table 7, 8). During 1977 and again in 1983, cattle left the river bottom to graze in the uplands. In 1977 little forage remained in riparian habitat, and in 1983 grasses were plentiful in the uplands.

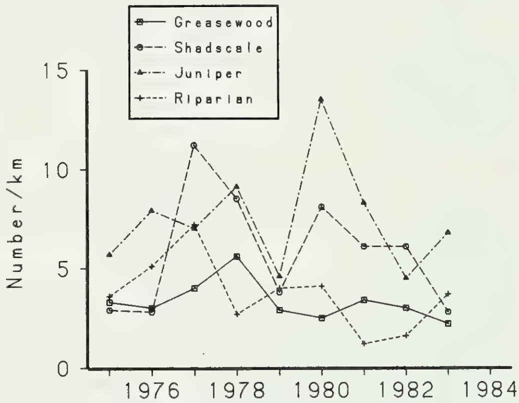

Fig. 12. Reptilian abundance in four vegetation types at Oil Tracts Ua-Ub, Uintah County, Utah.

Population Dynamics

The few amphibian species did not reflect any general trends, except that Ua-Ub habitat does not favor an abundant or diverse amphibian fauna. Among the reptiles the snake component was also limited in number but, for the most part, consistently encountered from year to year. Lizards were more abundant, perhaps the most abundant vertebrates at Ua-Ub. Abundance measured for all vertebrates included those observations made at zero point on the transect line. For birds and mammals, distance to the farthest observation was unlimited, but usually few individuals were seen beyond 100 m. For lizards maximum observable distance from the transect was 4 m.

Annual lizard population dynamics were mixed (Fig. 12). Although there were seemingly large changes, neither abundance, richness, nor diversity changed significantly from year to year.

TABLE 9. Spatial distribution of reptiles, birds, and mammals according to abundance, species richness, and species diversity at Oil Shale Tracts Ua-Ub. Letters signify differences at $p \leq 0.05$.

Vegetation type	Abundance ± SE	Richness ± SE	Diversity ± SE
	REPTILES June 1975–1983		
	Number/Kilometer	Number of species	H′
Greasewood	3 ± 0.3 a	4 ± 0.4	1.02 ± 0.09
Shadscale	6 ± 1.0 b	4 ± 0.6	1.14 ± 0.18
Juniper	7 ± 0.9 b	5 ± 0.2	1.33 ± 0.03
Riparian	4 ± 0.6 a	5 ± 0.6	1.31 ± 0.12
	BIRDS June 1975–1984		
	Number/kilometer	Number of species	H′
Greasewood	16 ± 2.0 a	21 ± 1.0 a	2.41 ± 0.08
Shadscale	13 ± 1.0 a	16 ± 1.0 b	2.22 ± 0.08 a
Juniper	18 ± 2.0 a	23 ± 1.0 a	2.60 ± 0.06 b
Riparian	82 ± 15.0 b	44 ± 2.0 c	2.59 ± 0.14 b
	MAMMALS (Lagomorpha, Rodentia, Carnivora, Artiodactyla) August 1975–1984		
	Number/Kilometer	Number of species	H′
Greasewood	3 ± 1.0	2 ± 0.3 a	0.18 ± 0.07 a
Shadscale	2 ± 0.6	2 ± 0.3	0.33 ± 0.10
Juniper	3 ± 0.7	3 ± 0.5	0.45 ± 0.11
Riparian	4 ± 2.0	3 ± 0.5 b	0.60 ± 0.14 b
	RODENTS August 1975–1984		
	Individuals/hectare	Number of species	H′
Greasewood	18 ± 3.0	5 ± 0.5 a	1.15 ± 0.10 a
Shadscale	15 ± 3.0 a	5 ± 0.5 ac	1.20 ± 0.07 a
Juniper	13 ± 3.0 a	7 ± 0.7 b	1.51 ± 0.13 b
Riparian	25 ± 6.0 b	4 ± 0.5 c	0.69 ± 0.11 c

Overall, reptiles were the most consistent and stable vertebrates at Ua-Ub despite desert blooms in 1975 and 1983, a drought in 1977, and the severe winters of 1979 and 1984.

Lizard abundance was concentrated in two dissimilar vegetation types, juniper and shadscale (Table 9). Juniper provided lizard populations with the following features: a high percentage of bare ground and rock (75%); shallow soils; low annual plant productivity; juniper trees, both live and dead, to serve as perches and nest sites; and additional vertical relief due to sandstone escarpments and randomly strewn boulders. Shadscale vegetation type east of Evacuation Creek did not meet any of the above criteria; however, a new site selected in 1977 did. Specifically it had 80% bare ground and rock, shallow soils, low annual plant productivity, and additional vertical relief from sandstone escarpments. Different were the absence of large boulders and only a few scattered juniper occurring at the new shadscale site, S 4 (see Fig. 7).

Similarity indices derived from Motyka et al. (1950) for reptilian species composition and abundance were used to compare within and between juniper and shadscale vegetation types. When all reptile populations in shadscale were sampled east of Evacuation Creek, species composition and abundance similarity averaged 88 ± 18% and 63 ± 12%, respectively. A new shadscale site west of Evacuation Creek compared to site S 1 at 34 ± 21% similarity in species composition and 13 ± 5% similarity in abundance. Comparing reptiles between the new shadscale site and juniper resulted in similarity of species composition and abundance at 82 ± 1% and 66 ± 3%, respectively. These values were not much different from similarities within juniper: 69 ± 7% for composition and 72 ± 4% for abundance. Using the flora as a sole criterion for delineating a vegetation type was disputed by the reptiles. Classifying a vegetation type based on physical and faunal as well as floral characteristics would be more appropriate for environmental assessment.

Reptiles were inactive from November through March, then dependent on daily weather conditions in April through October. Peak lizard activity occurred in June and de-

TABLE 10. Seasonal distribution of reptiles, birds, and mammals according to abundance, species richness, and species diversity at Oil Shale Tracts Ua-Ub. Letters signify differences at p ≤ 0.05.

Month	Abundance ± SE	Richness ± SE	Diversity ± SE
	REPTILES 1975–1981		
	Number/Kilometer	Number of species	H′
June	5 ± 0.5 a	5 ± 0.3	1.16 ± 0.07
August	4 ± 0.4 b	5 ± 0.3	1.09 ± 0.07
	BIRDS (Greasewood, Shadscale, Juniper Only) 1975–1981		
	Number/Kilometer	Number of species	H′
February	5 ± 1.0 a	5 ± 0.4 a	0.44 ± 0.08 a
April	12 ± 1.0 b	13 ± 2.0 b	1.46 ± 0.10 b
June	14 ± 1.0 b	19 ± 2.0 c	1.96 ± 0.06 c
August	10 ± 2.0 b	14 ± 2.0 b	1.53 ± 0.07 b
October	11 ± 2.0 b	8 ± 1.0 d	0.94 ± 0.09 d
	BIRDS (Riparian Only) 1975–1981		
	Number/Kilometer	Number of species	H′
February	20 ± 12.0 a	11 ± 1.0 a	1.18 ± 0.17 a
April	28 ± 3.0 a	27 ± 3.0 b	2.41 ± 0.08 b
June	63 ± 9.0 b	40 ± 4.0 c	2.42 ± 0.10 b
August	27 ± 4.0 a	30 ± 3.0 b	2.26 ± 0.12 bc
October	29 ± 6.0 a	18 ± 2.0 a	1.91 ± 0.17 c
	BATS 1977–1980		
	Individuals/Trap night	Number of species	H′
June	18 ± 2.0 a	5 ± 0.4 a	1.19 ± 0.09 a
August	11 ± 2.0 b	3 ± 0.3 b	0.91 ± 0.10 b
	MAMMALS (Lagomorpha, Rodentia, Carnivora, Artiodactyla) 1975–1981		
	Number/Kilometer	Number of species	H′
February	1 ± 0.4 a	2 ± 0.2	0.23 ± 0.06
April	1 ± 0.3 a	2 ± 0.2	0.26 ± 0.06
June	2 ± 0.4 b	2 ± 0.3	0.36 ± 0.08
August	3 ± 0.7 c	2 ± 0.2	0.31 ± 0.07
October	3 ± 0.9 c	2 ± 0.3	0.22 ± 0.06
	RODENTS 1975–1981		
	Individuals/100 Trap Night	Number of Species	H′
February	8 ± 2.0 a	3 ± 0.4 a	0.51 ± 0.14 a
April	14 ± 2.0 b	3 ± 0.3 b	0.75 ± 0.10 b
June	14 ± 1.0 b	4 ± 0.4 c	0.97 ± 0.10 c
August	15 ± 2.0 b	5 ± 0.3 c	1.01 ± 0.09 c
October	17 ± 2.0 b	4 ± 0.4 b	0.76 ± 0.09 b

clined by August (Table 10). About 30% of active lizards during August were juveniles.

Bird populations at Ua-Ub, especially those in riparian vegetation, were at high levels of abundance during 1975, 1982, and 1983 (Fig. 13); yet, when abundance in all vegetation types was analyzed, no significant annual differences were detectable. Nor were there any annual differences in species richness or species diversity; however, density, richness, and diversity did show annual differences during 1975–1981 (Steele et al. 1987). Nevertheless, the fact that peak avian abundance occurred in riparian vegetation during the years mentioned was evident. It was also evident that avian abundance and richness in riparian vegetation far exceeded the values found in upland vegetation, although juniper species diversity ranked it as a vegetation type equivalent to riparian (Table 9).

A masking effect of riparian bird populations led to an analysis of annual avian abundance in greasewood, shadscale, and juniper vegetation only. The results showed that bird abundance in upland vegetation during 1975 (23 birds/km) exceeded all years ($p \leq 0.05$) except 1983 (21 birds/km) and 1984 (18 birds/km). The abundance in

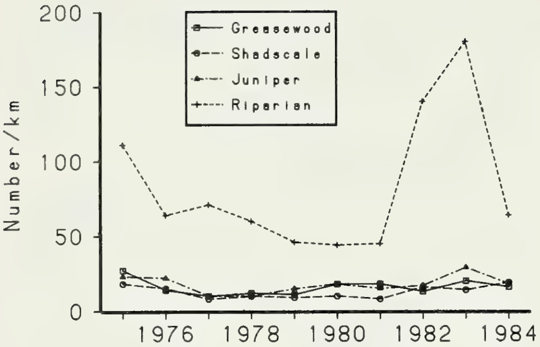

Fig. 13. Avian abundance in four vegetation types at Oil Shale Tracts Ua-Ub, Uintah County, Utah.

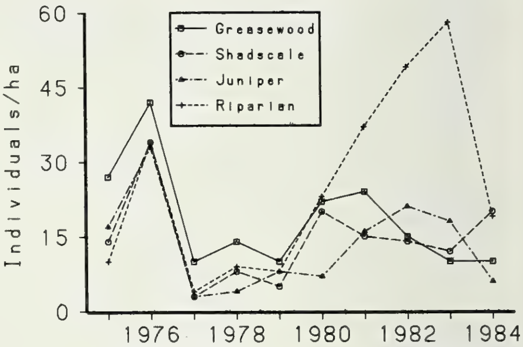

Fig. 14. Rodent density in four vegetation types at Oil Shale Tracts Ua-Ub, Uintah County, Utah.

1977 (9 birds/km) was lower than all other years ($p \leq 0.05$) except 1978 (10 birds/km), 1979 (12 birds/km), and 1984 (14 birds/km). The effect of the drought was reflected in bird abundance; however, change in species richness from year to year was imperceptible.

Seasonal changes in bird abundance and richness were also separated to eliminate the masking effect of riparian population. Riparian birds reached peak abundance in June, whereas upland bird populations reached a plateau in April and did not change appreciably through October (Table 10). Both riparian and upland populations were at peak richness in June, also when diversity was highest for upland birds; however, diversity of riparian birds did not differ from spring through late summer.

The large mammal community was so limited in species that the desert cottontail population dynamics (see Fig. 8) were essentially the community dynamics (Table 9 and 10). The bat community, on the other hand, was at highest abundance, richness, and diversity in June (Table 10). Annually, bat abundance was low during the 1977 drought (8 bats/trap night), then increased dramatically in 1978 (25 bats/trap night), and declined to abundance equivalent to 1977 in 1979 and 1980 ($p \leq 0.05$). This pattern mimicked that of aerial-feeding insectivores, i.e., nighthawks, swifts, and swallows ($p \leq 0.01$; $r = 0.976$).

The rodent community in all vegetation types responded in concert to changes in weather and subsequent changes in floral productivity (Fig. 14). Peak density in 1976 exceeded most years, especially 1977 through 1979 ($p \leq 0.05$). By 1980 densities returned to what now appears a median level. However, from 1981 through 1983 only riparian rodents, deer mice and voles, exceeded the median. Species richness also peaked in 1976 (eight species) compared to all years except 1975, 1981 and 1982 and was lowest during 1977 (three species) and 1979 (four species) ($p \leq 0.05$).

Riparian vegetation that supported the highest rodent densities also supported lowest richness and diversity at Ua-Ub; juniper vegetation that supported lowest densities supported the highest richness and diversity (Table 9). Although juniper was consistently noted for its low densities, it held the record for rodent biomass prior to the invasion and short stay by montane voles in riparian. Rodent abundance increased from February to April, then maintained from spring through the fall (Table 10). Species activity was highest during the summer and lowest in winter.

During the seven-year span of seasonal trapping, the vegetation type that supported the highest rodent abundance was greasewood ($p \leq 0.05$). The shift to high density in riparian coincided with flash floods depositing upland sandy alluvium (up to 18 in deep) over the moist silty loams. Although seasonal rodent sampling and annual density sampling agreed on annual and spatial distribution, seasonal sampling during August did not adequately predict density (Steele et al. 1984).

Measurable changes in weather, soil depth and type, foliage height profiles, and floral productivity resulted in significant changes in wildlife. Spatially amphibians lacked the appropriate conditions for abundant and diverse populations. Reptiles, however, though not represented by numerous species, did prefer juniper and certain attributes of shrub vegetation. Bird were attracted to the most structurally diverse and productive vegetation. Larger mammals tended to be best represented in riparian habitat; however, small rodent species avoided it.

Reptiles, most birds, and bats were most abundant and diverse when weather was moderate or tending toward hot and annual grasses, forbs, and insects were most abundant and diverse. Larger birds, i.e., raptors and waterfowl were active during early spring, whereas larger mammals and rodents were most abundant and diverse from late summer into fall. Shelter for raptors was not important, since usable nest sites exceeded raptor density. Waterfowl nesting activity preceded spring runoff, and by midsummer waterfowl were virtually absent. Cottontails and the other large mammals were most susceptible to winter conditions and also responded in kind to floral production, especially perennial shrub production that peaked in fall. Rodents followed the same pattern and were also subject to soil distribution.

Desert wildlife reached different levels of abundance, richness, and diversity at different seasons, in different vegetation types, and during different years. The directions taken appeared to be predictable if sufficient years and enough environmental variables are measured. Weather, shelter, food, and competition, in that order, will best predict wildlife population and community dynamics.

ACKNOWLEDGMENTS

My gratitude is extended to R. Madsen, J. Godlove, W. and N. Hale, R. and T. Anderson, and L. Page of WRSOC; P. Kung, B. Steele, R. Bayn, N. Preece, R. Miller, M. Sylvia, E. Parker, and S. VanderWall of Bio-Resources; and personnel of VTN, Inc., Aerovironment, Inc., and NPI, Inc., during monitoring of tracts Ua-Ub.

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COMPARISON OF VEGETATION PATTERNS RESULTING FROM BULLDOZING AND TWO-WAY CHAINING ON A UTAH PINYON-JUNIPER BIG GAME RANGE

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ABSTRACT.—Two adjacent mechanically treated pinyon-juniper (*Pinus* spp. and *Juniperus* spp.) big game winter range sites in central Utah were sampled in 1981 to estimate vegetational differences and tree mortality from the two treatments. One site was treated by selectively bulldozing in 1957 and the other was double chained in 1965. Both treatments significantly reduced tree and litter cover, whereas significant increases were found for native grasses and shrubs compared to a nearby untreated site. Juniper cover for the untreated site was 35.5% compared to only 1.4% for the bulldozed area and 4.1% for the two-way chained area. Browse species densities were increased by the mechanical treatments. The use of different mechanical treatments on separate smaller portions of critical areas of big game winter range would help provide: (1) for both long-term and short-term use of a critical wintering area, (2) greater overall productivity and carrying capacity, and (3) greater diversity by creating more edge effect between the differently treated and untreated areas.

Pinyon-juniper (*Pinus* spp. and *Juniperus* spp.) ranges cover roughly 30 million ha in the western United States (West et al. 1975). Since the mid-1950s, mechanical treatment of pinyon-juniper ranges to increase forage production has been extensive (Aro 1975, Phillips 1977, Plummer et al. 1968). Methods used to reduce tree competition include: cabling, one-way chaining, two-way chaining, bulldozing, windrowing, tree crushing, and burning (Arnold et al. 1964, Aro 1975, Plummer et al. 1960, 1968, 1970, Stoddart et al. 1975, Vallentine 1980). This paper evaluates differences in vegetational patterns following bulldozing and two-way chaining and seeding on adjacent sites in central Utah.

STUDY AREA AND METHODS

The study area is a pinyon-juniper big game winter range 2 km east of Holden, Millard County, Utah. Elevation is approximately 1,600 m. The area is classified as an upland stony loam range site. Soils are slightly calcareous with a pH of 6.9. Average yearly precipitation is about 37.5 cm, with most of it coming during the winter months. Slope is relatively constant and averages 7%. The aspect is southwesterly. Before treatment the area supported an open stand of juniper (*Juniperus osteosperma*) with an intermixture of cliffrose (*Cowania stansburiana*), big sagebrush (*Artemisia tridentata*), broom snakeweed (*Xanthocephalum sarothrae*), and some antelope bitterbrush (*Purshia tridentata*). Cheatgrass (*Bromus tectorum*) is the most prominent understory species on the control site. Other grasses and forbs are infrequent and produce little forage (Christensen et al. 1964).

The bulldozed site is owned and managed by the Utah Division of Wildlife Resources, and the two-way chained site is federally owned and managed by the USDI Bureau of Land Management (BLM). Bulldozing was used to eliminate trees while minimizing disturbance to cliffrose and big sagebrush on Utah Division of Wildlife Resources land (Christensen et al. 1964). These two shrub species are considered important winter browse for big game animals.

The nine species seeded on the bulldozed site, listed in Table 1, were either broadcast seeded or hand seeded into the depressions left by uprooted juniper trees (Plummer et al. 1960). Only crested wheatgrass (*Agropyron cristatum*) was seeded on the BLM site; 9 kg/ha of seed was applied during the chaining operation. Grazing has varied on the bulldozed site since treatment. It was rested from

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TABLE 1. Percent cover by species on bulldozed and two-way chained sites and adjacent untreated pinyon-juniper ranges. Amount of broadcasted seed is for the bulldozed site only.

Species	Treatment			Seeding rate[1] (kg/ha)
	Untreated	Bulldozed	Two-way	
ANNUALS				
Bromus tectorium	1.33^{a*}	3.85^{a}	2.97^{a}	
Total all annual species	1.33^{a}	4.05^{a}	3.31^{a}	
GRASSES				
Agropyron cristatum	0.00^{a}	0.19^{a}	4.96^{b}	1.59[2]
Agropyron spicatum	0.00^{a}	8.74^{b}	1.68^{a}	
Agropyron tricophorum	0.00^{a}	2.54^{b}	0.00^{a}	0.55
Poa secunda	0.41^{a}	2.01^{a}	0.79^{a}	
Total all grass species	0.46^{a}	13.68^{c}	8.31^{b}	
SHRUBS				
Artemisia tridentata	2.43^{a}	10.92^{a}	5.95^{a}	0.13[2]
Cowania stansburiana	3.00^{a}	4.24^{a}	3.68^{a}	0.01[2]
Xanthocephalum sarothrae	0.42^{a}	2.55^{a}	9.65^{b}	
Total all shrub species	5.85^{a}	18.17^{b}	19.40^{b}	
TREES				
Juniperus osteosperma	35.47^{a}	1.42^{b}	4.10^{b}	
Quercus gambelii	6.64^{a}	2.64^{a}	0.00^{a}	
Total all tree species	42.11^{a}	4.06^{b}	4.10^{b}	

*Values in the same row with different letters are significantly different at $P < .05$.

[1] Other seeded species were *Agropyron intermedium* (.48), *Medicago sativa* (0.08), *Atriplex canescens* (.17), *Chrysothamnus nauseosus* (.14), and *Purshia tridentata* (.34). The seeding rate for two-way chained site was *Agropyron cristatum* at 9 kg/ha.

[2] Some of the seed was hand-seeded into the depressions.

grazing from 1961 to 1962 and 1964 to 1965, but when grazed the stocking rate was 3.0 ha/per animal unit (AU) from 10 May to 15 June. Since treatment the two-way chained site has had a stocking rate of 4.5 ha/per animal unit (AU) from 1 May to 15 June. Both areas have been grazed by cattle throughout the study periods.

Treated areas were sampled by a single transect running across both treatments. This transect was 800 m long, with 400 m within each treatment. A second transect of 400 m was used to sample a nearby untreated area that was used as a control. Meter-square quadrats were placed at 10 m intervals along the transect. Total plant cover and cover by species were estimated using a variation of Daubenmire's (1959) cover class estimation technique. The variation consisted of adding a smaller cover class, 0% to 1%, so that the cover of small plants would not be overestimated. Percent cover of bare ground, litter, and rock were also estimated at each quadrat.

Density of trees and shrubs was evaluated by the use of a circular plot with an area of 50 m^2. This enlarged plot was centered on every third quadrat along the transect. In each enlarged plot, every shrub and tree was identified and assigned to a height and stem diameter class. Diameter of all trees was measured at 10 cm aboveground, and the largest stem of each multistemmed shrub was measured at approximately the same height. At least five juniper trees were cut near each transect and aged by growth rings. Regression analysis was used to correlate stem diameter with age. Evaluated parameters include: changes in species cover and composition, changes in tree and shrub density, and tree mortality resulting from treatment. Swept pellet group transects were used to indicate big game activity within the areas of treatment.

Composite soil samples were taken to a depth of 25 cm at every tenth quadrat along the transect. Soil texture, pH, and soluble salts were determined. Soils were also analyzed for nitrogen, phosphorus, potassium, calcium, magnesium, sodium, zinc, iron, manganese, and copper content.

RESULTS AND DISCUSSION

Total plant and litter cover were significantly reduced by both treatments when compared to the control (Table 2). However, total plant, bare ground, litter, and rock cover

TABLE 2. Percent cover of surface characteristics on bulldozed and two-way chained sites and adjacent untreated pinyon-juniper ranges.

	Treatment		
Characteristic	Untreated	Bulldozed	Two-way
Total plant cover	48.87^{a*}	37.90^{b}	35.48^{b}
Bare ground	25.08^{a}	27.07^{a}	33.12^{a}
Litter	27.22^{a}	15.33^{b}	16.59^{b}
Rock	4.47^{a}	3.37^{a}	3.19^{a}
Lifeform cover:			
Annual species	1.33^{a}	4.05^{a}	3.31^{a}
Forb species	.11^{a}	1.04^{a}	.36^{a}
Seeded grass species	.00^{a}	2.73^{a}	5.78^{a}
Native grass species	.46^{a}	10.95^{c}	2.53^{b}
Seeded shrub species**	5.43^{a}	12.43^{a}	9.64^{a}
Native shrub species	.42^{a}	2.64^{b}	9.76^{c}
Tree species	42.11^{a}	4.06^{b}	4.10^{b}

*Values in the same row with different letters are significantly different at $P < .05$.

**Included in the seed mixture were shrub species that also occur naturally on the site. These are shown as seeded in the table so that comparisons could be made between treatments.

were not significantly different between the two mechanical treatments. When these cover categories were compared, no significant differences existed between the two treatments, but visually and structurally they did appear quite different from each other. The treated sites supported significantly greater native grass and native shrub cover than the nearby untreated control site. Comparison between treatments showed that significant cover differences existed for the total of all grass species (Table 1). Crested wheatgrass had greater cover on the two-way chaining, whereas bluebunch wheatgrass (*Agropyron spicatum*) and sandberg bluegrass (*Poa secunda*) both were native and not seeded and exhibited greater cover on the bulldozed site. Pubescent wheatgrass (*Agropyron tricophorum*) showed good establishment and persistence on the bulldozed area.

Crested wheatgrass probably had greater cover because of its higher seeding rate on the two-way site, and the two-way chaining prepared an improved seedbed and covered the seed for better germination and establishment. Crested wheatgrass was also seeded on the bulldozed site, but it did not respond as well as the other two wheatgrasses after the bulldozing treatment. Bluebunch wheatgrass was probably suppressed by crested wheatgrass competition on the two-way chained site. The bulldozed site exhibited greater big sagebrush and cliffrose cover than the chained site, but the cover values were not significantly different between sites.

Juniper density was significantly lower on the bulldozed site (Table 3). There were 42% more trees on the two-way chained area than the bulldozed site. This would indicate that bulldozing to eliminate juniper in this area was probably more effective than chaining because the bulldozed treatment was done eight years previous to the two-way chaining and still had fewer juniper when sampled in 1981. In this study the bulldozing treatment killed 81% of the juniper, whereas double chaining killed only 54% when compared to the nearby control area. Aro (1975) reported a 95% to 100% kill when the trees were windrowed with a bulldozer and burned, whereas double chaining averaged 60% kill. Arnold et al. (1964) stated that double chaining results in a 50% to 80% kill of juniper trees.

Many researchers have noted that a major factor determining actual tree kill from mechanical treatments is the age structure of the juniper stand before treatment (Aro 1975, Skousen 1982, Stevens et al. 1975). Trees on the control area indicated that the stand was relatively young at the time of treatment. Of the trees sampled there, 40% were small, with stem diameters of 5 cm or less when the treatment took place. The presence of these small, flexible trees may explain why the chaining treatment was less effective than bulldozing. No significant differences were found between the sites for cliffrose and big sagebrush densities. Cliffrose cover was higher on the bulldozed site. This anomaly probably arose because surviving plants of

TABLE 3. Tree and shrub densities per hectare on bulldozed, two-way chained, and untreated pinyon-juniper ranges.

Species	Treatment		
	Untreated	Bulldozed	Two-way
TREES			
Juniperus osteosperma	771^a	428^b	734^a
Quercus gambelii	454^a	719^a	305^a
Total trees	1225^a	1147^a	1039^a
SHRUBS			
Artemisia tridentata	1351^a	2738^a	1943^a
Chrysothamnus nauseosus	21^a	244^a	30^a
Cowania stansburiana	429^a	597^a	963^a
Xanthocephalum sarothrae	389^a	934^a	5936^b
Total shrubs	2190^a	4513^a	8872^b

*Values in the same row with different letters are significantly different at $P < .05$.

cliffrose were much larger on the bulldozed site. Two-way chaining appears to have uprooted or broken off all large cliffrose plants (Christensen et al. 1964). Cliffrose plants were intentionally avoided on the bulldozed project. Broom snakeweed was six times more dense on the chained site, suggesting that increased soil disturbance may have allowed this invader species to spread (Arnold et al. 1964). For example, broom snakeweed made up 7% of the shrub cover for the untreated area, 14% of the shrub cover for the bulldozed area, and a high 50% of the shrub cover for the two-way chained area.

Only one soil factor was significantly different between untreated, bulldozed, and two-way chained sites (Table 4). Phosphorus concentrations were significantly lower on the bulldozed site than on the untreated or two-way chained areas.

Utah Wildlife Resource conservation officers reported that swept pellet group transects showed big game activity to be two to three times heavier on the bulldozed site than on the two-way chained area. Some years, e.g. 1977, big game use was 13 times heavier on the bulldozed site than on the two-way chained areas (Brent Olsen, data on file).

It has been suggested that the preferential use of the bulldozed site by deer was related to the greater height of the cliffrose. On the two-way chained area, 75% of the cliffrose individuals were under 1 m tall, and all cliffrose plants were under 1.5 m tall. On the bulldozed site, 50% of the cliffrose plants were under 1 m tall, 30% were between 1 and 2 m, and 20% were over 2 m. The deer apparently preferred the bulldozed site where the larger cliffrose plants provided security cover as well as a variety of forage.

Even though the study sites were treated eight years apart, some generalizations are worth noting. Although bulldozing costs are 1.5 to 2 times greater (depending on tree density) than two-way chaining (Bill Davis, personal communication), bulldozing was a practical and effective method for juniper removal on this site. Widemann and Cross (1981) found that bulldozing light to moderate stands of juniper in Texas with a small, low-powered crawler tractor was an economical alternative. Their cost varied from $6 to $50 per ha. The trees on this area did not constitute a closed stand, but the bulldozing treatment left Gambel oak (*Quercus gambelii*), a sprouting species, undisturbed. Bulldozing also allowed minimal disturbance to desired understory species. Cliffrose, an important cover and browse species for big game in this area, was left intact and big sagebrush populations were rejuvenated following treatment and seeding. Because big game showed a two- to threefold preference for bulldozed versus the two-way chained site, restoration projects on pinyon-juniper big game ranges in this area should consider the feasibility of using this method. However, because cliffrose density was increased by double chaining, the two-way chained area should become increasingly more valuable to big game in the future as the cliffrose becomes more mature.

Within areas of critical winter range, it would be advisable to apply different mechanical treatments to different sections of the range. Bulldozed areas could be used by wildlife immediately because the understory is left minimally disturbed (assuming an understory of desirable remnant plants are present for subsequent release and reseeding themselves), whereas

TABLE 4. Soil data on bulldozed, two-way chained, and adjacent untreated pinyon-juniper ranges.

Characteristic	Treatment		
	Untreated	Bulldozed	Two-way
Texture	Clay loam	Loam	Loam
Depth, cm	16.5^{a*}	15.0^{a}	14.0^{a}
pH	6.5^{a}	6.8^{a}	6.9^{a}
Soluble salts, ppm	608.0^{a}	590.0^{a}	560.0^{a}
Phosphorus, ppm	36.2^{a}	8.7^{b}	27.1^{a}
Potassium, ppm	300.7^{a}	234.0^{a}	228.0^{a}
Calcium, ppm	6756.0^{a}	9500.0^{a}	10075.0^{a}
Magnesium, ppm	381.2^{a}	300.0^{a}	275.0^{a}
Sodium, ppm	43.9^{a}	86.5^{a}	83.0^{a}
Zinc, ppm	1.6^{a}	1.0^{a}	1.6^{a}
Iron, ppm	76.0^{a}	57.3^{a}	37.5^{a}
Manganese, ppm	61.5^{a}	49.0^{a}	33.6^{a}
Copper, ppm	1.1^{a}	1.0^{a}	1.2^{a}
% Nitrogen	0.2^{a}	0.2^{a}	0.2^{a}

*Means within rows with the same letter are not significantly different at $P < .05$.

chained areas would become more beneficial as the plant species mature. A regional approach should be developed that would allow areas to be treated by different mechanical techniques (varying degrees of disturbance) while leaving some areas undisturbed for a better balanced use of the resource through time. These combined treatment effects would provide for: (1) both short-term and long-term use of the treated areas by various livestock and wildlife species because of the varying stages of community development that the mechanical treatments induce, (2) greater overall productivity and carrying capacity, and (3) greater edge effect between differentially treated and undisturbed areas.

ACKNOWLEDGMENTS

This research was made possible with federal funds for wildlife restoration provided through Pittman-Robertson Project W-82-R, Job 1, in cooperation with the Intermountain Research Station, USDA Forest Service, and the Utah Division of Wildlife Resources.

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VERTEBRATE FAUNA OF THE IDAHO NATIONAL ENVIRONMENTAL RESEARCH PARK

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ABSTRACT.—The relative abundance, habitat use, and seasonal occurrence are reported for the 6 fish, 1 amphibian, 9 reptile, 164 bird, and 39 mammal species recorded on the Idaho National Environmental Research Park in southeastern Idaho.

The Idaho National Engineering Laboratory (INEL) is an energy research and development site administered by the U.S. Department of Energy (DOE). The Energy Reorganization Act of 1974 ordered the U.S. Energy Research and Development Administration (precursor to DOE) to engage in environmental research related to the development of energy sources to advance the goals of restoring, protecting, and enhancing environmental quality. The INEL was designated the nation's second National Environmental Research Park (NERP) in 1975 to satisfy this directive. The NERP provides a controlled, protected, outdoor laboratory for environmentally related research to help achieve national environmental goals as stated in the National Environmental Policy Act (NEPA) of 1969. The NERP charter presents broad objectives which, in part, require that each NERP serve as a bench mark for quantitatively assessing and predicting the environmental impact of man's activities. The compilation of baseline data, including species lists and identification of ecological communities, is fundamental to the NERP objectives. Much of the research on individual species of wildlife found on the Idaho NERP has been published in the scientific literature or presented in theses, dissertations, or reports (vide Markham 1973, 1978, 1983). This paper represents a consolidation of those findings which, combined with unpublished information, provide baseline data on the abundance, distribution, habitat preference and seasonal occurrence of the vertebrate species recorded on the Idaho NERP.

STUDY AREA

The INEL was established by the U.S. Atomic Energy Commission as the National Reactor Testing Station in the late 1940s. Since 1949 the land composing the Idaho NERP has been closed to public access, thereby providing wildlife habitat that has remained relatively undisturbed for 35 years.

The NERP occupies about 2,305 km^2 of sagebrush-dominated rangeland on the upper Snake River Plain in portions of Bonneville, Bingham, Butte, Clark, and Jefferson counties. The INEL is approximately 48 km west of Idaho Falls, Bonneville County, Idaho. With the exception of two large buttes of volcanic origin near the southeastern boundary, and several small cinder cones, craters, and exposed lava ridges scattered over the site, the topography of most of the NERP is flat to gently rolling and typical of the Columbian Plateau Province (Atwood 1970). The mean elevation is 1,490 m ASL. Three predominately north-south mountain ranges, rising to 3,370 m ASL, border the NERP to the north and west (Fig. 1). The intervening valleys and the Snake River Plain itself provide migration corridors to, or across, the Site. Soils are derived mostly from silicic volcanics and Paleozoic rocks from the surrounding mountains. These are primarily aeolian sandy loams and loess underlain by undifferentiated basalt

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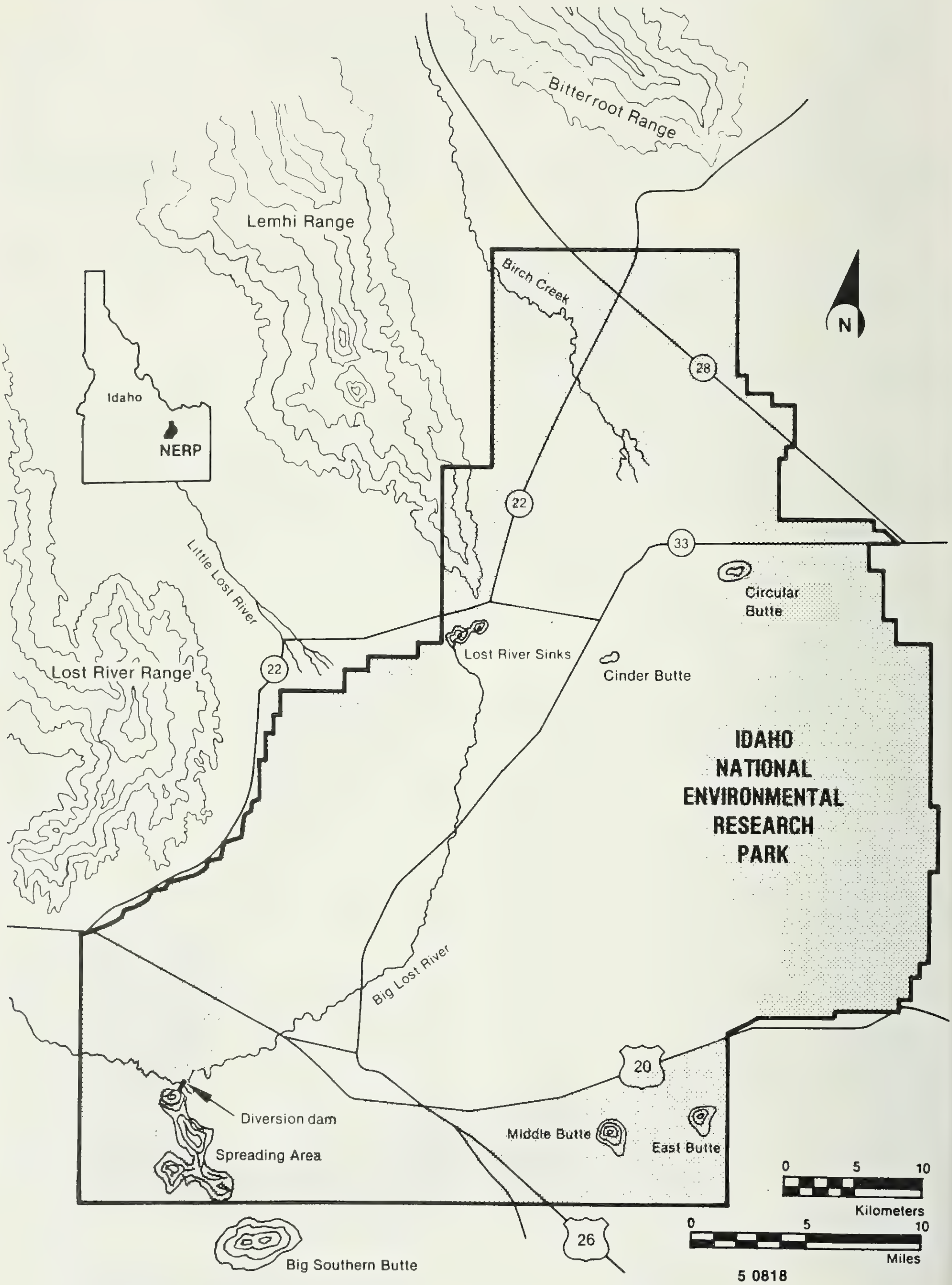
Bitterroot Range
Lemhi Range
Birch Creek
28
N
Idaho
NERP
22
33
Little Lost River
Circular Butte
Lost River Sinks
Cinder Butte
Lost River Range
22
IDAHO NATIONAL ENVIRONMENTAL RESEARCH PARK
Big Lost River
20
Diversion dam
Spreading Area
Middle Butte
East Butte
0 5 10 Kilometers
0 5 10 Miles
26
Big Southern Butte
5 0818

Fig. 1. Landmarks, roadways, and watercourses on the Idaho National Environmental Research Park and environs in southeastern Idaho. The area of the park open to livestock grazing is shaded.

atop a rhyolite foundation. The climate is characterized by hot summers and cold winters. Maximum and minimum temperatures recorded from 1950 to 1983 are 39 and −44 C, respectively. Annual precipitation over the past 34 years averaged 21.6 cm (Range: 11.4–36.6 cm), coming mostly from spring rain or snow storms in April, May, and June, with a smaller peak resulting from snowfall during December and January.

Surface water is limited on the Idaho NERP. The Big Lost River enters the southwest corner of the INEL, flows northward about 50 km, and ultimately percolates into the Snake River aquifer at the sinks near Howe, Idaho (Fig. 1). When filled, the sinks provide about 260 surface ha of aquatic habitat. Because of annual variations in the snowpack, offsite irrigation demands upstream, and the porosity of the stream bed, the Big Lost River does not flow across the NERP throughout every summer. In some years water never reaches the sinks. Water is also diverted from the Big Lost River into four spreading areas in the southwest corner of the INEL (Fig. 1) to prevent ice jams and flooding of some INEL facilities during the winter and spring runoff. Thus a series of ephemeral shallow lakes of up to 919 ha in total size is generally present during the spring peak of bird migration. Other natural water sources on the Idaho NERP are the Little Lost River and Birch Creek. Both of these streams are currently diverted offsite for agricultural irrigation and only rarely flow onto the INEL. Several 0.2–5.0 ha man-made ponds occur near facilities on site. In aggregate these provide approximately 15 ha of additional aquatic habitat.

Although McBride et al. (1978) described 20 distinct vegetative cover types on the INEL, nearly 87% of the NERP is shrub-steppe habitat. About 7% is grassland, and about 3% is juniper woodland. Aquatic and riparian habitat and irrigated lawns at facility complexes account for the remaining 3%. The dominant and most conspicuous vegetation is big sagebrush (*Artemisia tridentata*). Other locally important shrubs are rabbitbrush (*Chrysothamnus nauseosus* and *C. vicidiflorus*), winterfat (*Ceratoides lanata*), shadscale saltbush (*Atriplex confertifolia*), Nuttall saltbush (*A. nutallii*), and gray horsebrush (*Tetradymia canescens*) (Anderson and Holte 1981, Harniss and West 1973). The more abundant grasses include bottlebrush squirreltail (*Elymus elymoides*: formerly *Sitanion hystrix*), needle and thread grass (*Stipa comata*), Indian ricegrass (*Oryzopsis hymenoides*), Great Basin wild rye (*Leymus cinereus*: formerly *Elymus cinereus*), thickspike wheatgrass (*Elymus lanceolatus*: formerly *Agropyron dasystachyum*), and bluebunch wheatgrass (*Elytrigia spicata*: formerly *A. spicatum*). Native tree species are limited to junipers (*Juniperus osteosperma* and *J. scopulorum*) near the southeast and northwest portions of the NERP, and plains cottonwood (*Populus deltoides*), narrow-leaved cottonwood (*P. angustifolia*), and several species of willow (*Salix* spp.) along the Big Lost River and Birch Creek. Russian olive (*Elaeagnus angustifolia*) and several other introduced species of deciduous and evergreen trees have been planted near most of the INEL facilities. Lawns composed of *Poa* spp. are maintained at most of the facility complexes. Approximately 4,000 ha of the INEL were seeded with crested wheatgrass (*Agropyron cristatum* and *A. desertorum*) in the late 1950s and early 1960s. Reinvasion by native shrub-steppe vegetation has been slow, and these plantings persist mostly as monocultures (Marlette 1982). Jeppson and Holte (1978) listed a total of 389 vascular plant species on the INEL. None are classified as threatened or endangered at either the federal or state level (Cholewa and Henderson 1984). The periphery of the NERP, representing nearly 65% of the total area, is open to seasonal cattle and sheep grazing regulated by the U.S. Department of the Interior Bureau of Land Management (Fig. 1).

The geology, topography, vegetation, climate, and recent history of Idaho NERP previously have been described in detail (Anderson and Holte 1981, Atwood 1970, Harniss and West 1973, Nace et al. 1972, 1975, McBride et al. 1978).

Public access to the Idaho NERP is restricted. Except for scientific purposes and periodic predator control, the collection of flora and fauna is prohibited.

METHODS

Past and present ecological studies conducted on the INEL and correspondence and interviews with INEL researchers and per-

TABLE 1. Fishes recorded on the Idaho National Environmental Research Park.

Taxa	Distribution	Abundance[1]
SALMONIFORMES		
Salmonidae		
Kokanee Salmon, *Oncorhynchus nerka*	Big Lost River	Uncommon
Rainbow Trout, *Salmo gairdneri*	Big Lost River	Common
Brook Trout, *Salvelinus fontinalis*	Big Lost River	Uncommon
Mountain Whitefish, *Prosopium williamsoni*	Big Lost River	Common
CYPRINIFORMES		
Cyprinidae		
Speckled Dace, *Rhinichthys osculus*	Big Lost River	Uncommon
PERCIFORMES		
Cottidae		
Shorthead Sculpin, *Cottus confusus*	Big Lost River	Common

[1] See text for definitions of abundance terms.

sonnel provided the data presented in this paper. Species inventories and population assessments on the Idaho NERP have been published for small mammals (Allred 1973), herpetofauna (Sehman and Linder 1978), and raptors (Craig 1979). Additional data on these and other taxa were gleaned from numerous sources. Those that provided limited but useful information germane to this paper and not cited elsewhere in the text included theses and dissertations (Craig 1977, Fuller 1981, Gleason 1978, Hoskinson 1977, Johnson 1977, Peterson 1982, and Reynolds 1978) and technical publications (Bailey 1974, Best and Peterson 1982, Craig 1978, Craig and Renn 1977, Halford and Millard 1978, Powers and Craig 1976, and Reynolds and Trost 1980).

Moreover, current and previous NERP researchers were encouraged to record observations of vertebrates encountered incidental to their research activities and, from their experience, to indicate the relative abundance and distribution of these species on the Idaho NERP. Informal interviews with INEL Site services and security personnel provided additional information.

The relative abundance, distribution, and habitat use for all native and introduced vertebrate species recorded on the Idaho NERP are presented. Abundance ratings were used to indicate relative numbers of a species during the season(s) it was recorded on the Idaho NERP. Sehman and Linder (1978) and Overton (1977) provided abundance and residence status for herpetofauna and fishes, respectively.

Abundance ratings for terrestrial homeotherms are often biased in favor of conspicuous and diurnal species, especially when observations incidental to other projects are the source of data. To reduce this bias, former and current INEL ecological researchers subjectively rated the abundance of each bird and mammal species, based on personal experience. Ratings were from 1 to 10, 1 representing a very rare sighting and 10 indicating an abundant species. A mean value for each species was calculated. Because the ratings for some species ranged widely (i.e., from 1 to 9), a category termed *occasional* or *local* was included (cf Stephens and Reynolds 1983). All abundance classes assumed that a qualified biologist exerted a reasonable effort to search or sample the proper habitat at the appropriate time of year.

Abundance ratings were:

1. Abundant—Very numerous and certain to be seen or sampled: a mean rating of 8.1–10.0.
2. Common—Likely but not certain to be observed or sampled: a mean rating of 5.1–8.0.
3. Uncommon—Found in limited numbers, not likely to be sampled or observed: mean rating of 2.1–5.0.
4. Occasional or local—A species that is not always present or is restricted in distribution: a difference between the high and low response of 7 or more.
5. Rare—A species that has a range including all or part of the Idaho NERP but has been documented ≤ seven times on site: mean rating of 0.1–2.0.
6. Vagrant or accidental—A species that is not expected to occur on the Idaho NERP but has been recorded there (e.g., Black-legged Kittiwake [*Rissa tridactyla*]).

Habitats listed for each species closely follow those presented by Trost et al. (1977) and Stephens and Reynolds (1983). The designation "sitewide" indicates that a particular species was ubiquitous on the Idaho NERP. Unless otherwise noted, taxonomic nomen-

TABLE 2. Herptiles recorded on the Idaho National Environmental Research Park.

Taxa	Distribution and habitat	Abundance[1]
ANURA		
Pelobatidae		
Great Basin Spadefoot Toad, *Spea intermontana*[2]	Big Lost River and sinks	Common
SQUAMATA		
Iguanidae		
Leopard Lizard, *Gambelia wislizenii*[3]	NE NERP; sandy areas	Local
Short-horned Lizard, *Phrynosoma douglassi*	Sitewide; shrub-steppe	Abundant
Sagebrush Lizard, *Sceloporus graciosus*	Sitewide; shrub-steppe	Abundant
Scincidae		
Western Skink, *Eumeces skiltonianus*	South NERP	Rare
Boidae		
Rubber Boa, *Charina bottae*	Unknown	Accidental
Colubridae		
Desert Striped Whipsnake, *Masticophis taeniatus*	NE NERP; shrub-steppe	Uncommon
Gopher Snake, *Pituophis melanoleucus*	Sitewide; shrub-steppe	Common
Western Garter Snake, *Thamnophis elegans*	Sitewide; all habitats	Uncommon
Viperidae		
Western Rattlesnake, *Crotalus viridis*	Sitewide; shrub-steppe	Common

[1] See text for definitions of abundance terms.

[2] Collins et al. (1978) list this as *Scaphiophus intermontanus*.

[3] Collins et al. (1978) place this in the genus *Crotaphytus*.

clature for fish, amphibians and reptiles, birds, and mammals follows Simpson and Wallace (1978), Nussbaum et al. (1983), American Ornithological Union (1983), and Jones et al. (1982), respectively.

RESULTS AND DISCUSSION

A total of 219 vertebrate species were recorded on the Idaho NERP. Only six species of fish (Table 1) were identified. Four of these were game fish (all salmonids), and two were nongame species. Species inventories of fish were incidental to a study on the density and distribution of salmonid fishes in the Big Lost River (Overton 1977) and a game fish salvage and transplant operation conducted by the Idaho Department of Fish and Game. Because both of those activities primarily concerned game fish, the records of nongame species actually present in the Big Lost River on the NERP may be incomplete. Contrariwise, the low species richness may indeed be accurate, caused by annual and seasonal fluctuations in the flow rate of the river. Overton (1977) attributed decreases in salmonid populations on the NERP directly to: (1) abnormally high discharge in the spring and (2) low or nonexistent flows during both the winter and summer. Diversion practices to control flooding typically reduce the flow in the winter months, whereas low summer flows result from upstream irrigation demands and are generally accompanied by elevated water temperatures. Additional efforts may be needed to completely inventory fish populations on the Idaho NERP.

One amphibian and nine reptiles were recorded on the Idaho NERP (Table 2). The spadefoot toad (*Spea intermontana*) was reported from the Big Lost River as well as the Lost River Sinks and the diversion spreading area (Fig. 1).

There is only one confirmed record for the rubber boa (*Charina bottae*) on the Idaho NERP. Concentrations of leopard lizards (*Gambolia wislizenii*) and desert stiped whipsnakes (*Masticophis taniatus*) were only found in the northeast portion of the NERP, near Circular Butte and Cinder Butte, respectively (Linder and Sehman 1978) (Fig. 1). The former species is evidently restricted to areas of sandy soils. The latter is more widespread but limited in numbers away from Cinder Butte (Sehman and Linder 1978). The western skink (*Eumeces skiltonianus*) is confined to isolated locations on the southern half of the NERP, possibly because of increased microhabitat moisture requirements (Sehman and Linder 1978). The remainder of the herptiles species listed are either sitewide in distribution or found in the shrub-steppe habitat that

TABLE 3. Avifauna recorded on the Idaho National Environmental Research Park.

Taxa	Abundance[1], season, and breeding status[2]	Habitat[3]
Gaviiformes		
Gaviidae		
Common Loon, *Gavia immer*	M5	w
Podicipediformes		
Podicipedidae		
Pied-billed Grebe, *Podilymbus podiceps*	S5, M5	w
Horned grebe, *Podiceps auritus*	M5	w
Eared grebe, *P. nigricollis*	B5, M3, W3	w
Western Grebe, *Aechmophorus occidentalis*[4]	S5, M5	w
Pelecaniformes		
Pelecanidae		
American White Pelican, *Pelecanus erythrorhynchos*	M5	w
Ciconiiformes		
Ardeidae		
American Bittern, *Botaurus lentiginosus*	S5, M5	w
Great Blue Heron, *Ardea herodias*	S5, M5	w
Great Egret, *Casmerodius albus*	S5, M5	w
Green-backed Heron, *Butorides striatus*	S6, M6	w
Threskiornithidae		
White-faced Ibis, *Plegadis chihi*[5]	S5, M5	w
Anseriformes		
Anatidae		
Tundra Swan, *Cygnus columbianus*	M5	w
Snow Goose, *Chen caerulescens*	M5	w
Canada Goose, *Branta canadensis*	S3, M3	w
Wood Duck, *Aix sponsa*	S6, M5	w
Green-winged Teal, *Anas crecca*	S5, M5	w
Mallard, *A. platyrhynchos*	B2, M2, W3	w
Northern Pintail, *A. acuta*	S3, M3	w
Blue-winged Teal, *A. discors*	B2, M3	w
Cinnamon Teal, *A. cyanoptera*	S3, M3	w
Northern Shoveler, *A. clypeata*	B3, M3	w
Gadwall, *A. strepera*	S3, M3	w
American Wigeon, *A. americana*	S3, M3	w
Canvasback, *Aythya valisineria*	B5, M5	w
Redhead, *A. americana*	S5, M5, W5	w
Ring-necked Duck, *A. collaris*	S5, M5	w
Lesser Scaup, *A. affinis*	S5, M3, W3	w
Common Goldeneye, *Bucephala clangula*	S5, M3, W3	w
Barrow's Goldeneye, *B. islandica*	S6, M5	w
Bufflehead, *B. albeola*	S5, M3	w
Common Merganser, *Mergus merganser*	S3, M5	w
Ruddy Duck, *Oxyura jamaicensis*	B5, M3	w
Falconiformes		
Cathartidae		
Turkey Vulture, *Cathartes aura*	S3, M3, W6	sw
Accipitridae		
Osprey, *Pandion haliaetus*[5]	M5	w
Bald Eagle, *Haliaeetus leucocephalus*[6]	M5, W3	sw
Northern Harrier, *Circus cyaneus*	R2	sw
Sharp-shinned Hawk, *Accipiter striatus*[4]	S5, M5, W5	sw
Cooper's Hawk, *A. cooperii*	S3, M5, W5	sw
Northern Goshawk, *A. gentilis*	S5, M5, W5	sw
Swainson's Hawk, *Buteo swainsoni*	B3, M3, W5	sw
Red-tailed Hawk, *B. jamaicensis*	B3, M3, W5	sw
Ferruginous Hawk, *B. regalis*[5,7]	B3, M3, W5	sw
Rough-legged Hawk, *B. lagopus*	S6, M2, W2	sw
Golden Eagle, *Aquila chrysaetos*	B3, M4, W2	sw
Falconidae		
American Kestrel, *Falco sparverius*	B2, M2, W3	sw
Merlin, *F. columbarius*[5]	R5	sw

Table 3 continued.

Taxa	Abundance[1], season, and breeding status[2]	Habitat[3]
Peregrine Falcon, *F. peregrinus*[6]	S5, M5, W5	sw
Gyrfalcon, *F. rusticolus*[7]	M6	sw
Prairie Falcon, *F. mexicanus*[5]	R3	sw
GALLIFORMES		
Phasianidae		
Gray Partridge, *Perdix perdix*	R3	g, ss, f
Chukar, *Alectoris chukar*	R3	g, ss
Ring-necked Pheasant, *Phasianus colchicus*	R3	g, ss
Blue Grouse, *Dendragapus obscurus*	S6	f
Sage Grouse, *Centrocercus urophasianus*	R2	ss, g, f
GRUIFORMES		
Rallidae		
Sora, *Porzana carolina*	B5, M5	w, f
American Coot, *Fulica americana*	R3	w
CHARADRIIFORMES		
Charadriidae		
Killdeer, *Charadrius vociferus*	B2, M2	sw
Recurvirostridae		
American Avocet, *Recurvirostra americana*	S2, M3	w
Scolopacidae		
Greater Yellowlegs, *Tringa melanoleuca*	M5	w
Lesser Yellowlegs, *T. flavipes*	S5, M5	w
Solitary Sandpiper, *T. solitaria*	S5, M3	w
Willet, *Catoptrophorus semipalmatus*	S3, M3	w, ss
Spotted Sandpiper, *Actitis macularia*	S3, M3	w
Long-billed Curlew, *Numenius americanus*[4,5]	S3, M3	w, ss
Marbled Godwit, *Limosa fedoa*	S3, M5	w
Least Sandpiper, *Calidris minutilla*	S5, M5	w
Long-billed Dowitcher, *Limnodromus scolopaceus*	M5	w
Common Snipe, *Gallinago gallinago*	S5, M5	w
Wilson's Phalarope, *Phalaropus tricolor*	S3, M3	w
Red-necked Phalarope, *P. lobatus*	M5	w
Laridae		
Franklin's Gull, *Larus pipixcan*	S3, M3	w, ss
Bonaparte's Gull, *L. philadelphia*	M5	w
Ring-billed Gull, *L. delawarensis*	S3, M3	w, ss, g
California Gull, *L. californicus*	S5, M3	w, ss
Herring Gull, *L. argentatus*	S3, M3	w, ss, g
Black-legged Kittiwake, *Rissa tridactyla*	W6	w
Caspian Tern, *Sterna caspia*	M5	w
Forster's Tern, *S. forsteri*	S5	w
Black Tern, *Chlidonias niger*	S5, M5	w
COLUMBIFORMES		
Columbidae		
Rock Dove, *Columba livia*	R2	sw
Mourning Dove, *Zenaida macroura*	B1, M3, W5	sw
STRIGIFORMES		
Strigidae		
Great Horned Owl, *Bubo virginianus*	R3	sw
Snowy Owl, *Nyctea scandiaca*	W5	sw
Burrowing Owl, *Athene cunicularia*[5]	B3, M3, W6	ss, g
Long-eared Owl, *Asio otus*	B4, M4	d
Short-eared Owl, *A. flammeus*[4]	B3, M3	ss, g
Northern Saw-whet Owl, *Aegolius acadicus*	S6, M6, W6	sw
CAPRIMULGIFORMES		
Caprimulgidae		
Common Nighthawk, *Chordeiles minor*	B2, M3	sw
APODIFORMES		
Apodidae		
White-throated Swift, *Aeronautes saxatalis*	S5	d

Table 3 continued.

Taxa	Abundance[1], season, and breeding status[2]	Habitat[3]
Trochilidae		
Rufous Hummingbird, *Selasphorus rufus*	S3, M3	d
CORACIIFORMES		
Alcedinidae		
Belted Kingfisher, *Ceryle alcyon*	S3, M3	w
PICIFORMES		
Picidae		
Downy Woodpecker, *Picoides pubescens*	B5, M5	d
Northern Flicker, *Colaptes auratus*	B3, M3	d
PASSERIFORMES		
Tyrannidae		
Olive-sided Flycatcher, *Contopus borealis*	S5, M5	d
Western Flycatcher, *Empidonax difficilis*	S5	d
Say's Phoebe, *Sayornis saya*	B3, M3	ss, d, f, j
Ash-throated Flycatcher, *Myiarchus cinerascens*	S5	d
Western Kingbird, *Tyrannus verticalis*	B3, M3	f, d, j
Eastern Kingbird, *T. tyrannus*	B3, M3	f, d, j
Alaudidae		
Horned Lark, *Eremophila alpestris*	R2	g, ss
Hirundinidae		
Tree Swallow, *Tachycineta bicolor*	B3, M3	d, j
Violet-green Swallow, *T. thalassina*	B4, M4	d, j
Northern Rough-winged Swallow, *Stelgidopteryx serripennis*	B3, M3	d, j
Bank Swallow, *Riparia riparia*	B5, M3	d, j
Cliff Swallow, *Hirundo pyrrhonota*	B2, M2	d, j
Barn Swallow, *H. rustica*	B2, M3	d, j
Corvidae		
Clark's Nutcracker, *Nucifraga columbiana*	S4, M4, W5	j
Black-billed Magpie, *Pica pica*	R2	sw
American Crow, *Corvus brachyrhynchos*	R3	sw
Common Raven, *C. corax*	R3	sw
Troglodytidae		
Rock Wren, *Salpinctes obsoletus*	B3, M3	ss
Canyon Wren, *Catherpes mexicanus*	S5, M5	ss
House Wren, *Troglodytes aedon*	R3	d
Muscicapidae		
Ruby-crowned Kinglet, *Regulus calendula*	M3, W6	d
Western Bluebird, *Sialia mexicana*[4]	S5, M5	ss
Mountain Bluebird, *S. currucoides*	S3, M3	ss
Townsend's Solitaire, *Myadestes townsendi*	S5, M5	d
American Robin, *Turdus migratorius*	B2, M2	sw
Varied Thrush, *Ixoreus naevius*	W6	ss
Mimidae		
Northern Mockingbird, *Mimus polyglottos*	S6	j
Sage Thrasher, *Oreoscoptes montanus*	B2, M2	ss
Motacillidae		
Water Pipit, *Anthus spinoletta*	M5	ss
Bombycillidae		
Bohemian Waxwing, *Bombycilla garrulus*	S3, M2, W3	f, d
Cedar Waxwing, *B. cedrorum*	S5, M3, W5	f, d
Laniidae		
Northern Shrike, *Lanius excubitor*	M3, W5	sw
Loggerhead Shrike, *L. ludovicianus*[4]	B3	ss

Table 3 continued

Taxa	Abundance[1], season, and breeding status[2]	Habitat[3]
Sturnidae		
European Starling, *Sturnus vulgaris*	R3	sw
Vireonidae		
Warbling Vireo, *Vireo gilvus*	S5, M5	d
Emberizidae		
Yellow Warbler, *Dendroica petechia*[4]	B5, M3	d
Yellow-rumped Warbler, *D. coronata*	S3, M3	d
Townsend's Warbler, *D. townsendi*	M5	d
American Redstart, *Setophaga ruticilla*	M6	f
Common Yellowthroat, *Geothlypis trichas*	S5	d
Wilson's Warbler, *Wilsonia pusilla*	S5, M5	d
Yellow-breasted Chat, *Icteria virens*	S5	d
Western Tanager, *Piranga ludoviciana*	S3, M3	d
Black-headed Grosbeak, *Pheucticus melanocephalus*	S5, M5	sw
Lazuli Bunting, *Passerina amoena*	S5, M5	d
Green-tailed Towhee, *Pipilo chlorurus*	S3, M3	ss
Rufous-sided Towhee, *P. erythrophthalmus*	S3, M3	sw
Chipping Sparrow, *Spizella passerina*	M5	f, d, ss
Brewer's Sparrow, *S. breweri*	B2, M2	ss
Vesper Sparrow, *Pooecetes gramineus*	B3, M3	g, ss
Lark Sparrow, *Chondestes grammacus*	S3, M5	sw
Black-throated Sparrow, *Amphispiza bilineata*	S5, M5	ss
Sage Sparrow, *A. belli*	B2, M2	ss
Lark Bunting, *Calamospiza melanocorys*	S5, M5	ss
Savannah Sparrow, *Passerculus sandwichensis*	S5, M3	d, g
Song Sparrow, *Melospiza melodia*	S5, M3	d
White-crowned Sparrow, *Zonotrichia leucophrys*	M4	ss
Dark-eyed Junco, *Junco hyemalis*	M3	sw
Snow Bunting, *Plectrophenax nivalis*	W5	g, ss
Red-winged Blackbird, *Agelaius phoeniceus*	B3, M3	w, ss
Western Meadowlark, *Sturnella neglecta*	B2, M2, W3	g, ss
Yellow-headed Blackbird, *Xanthocephalus xanthocephalus*	B4, M3	w,d
Brewer's Blackbird, *Euphagus cyanocephalus*	B2, M2, W5	sw
Brown-headed Cowbird, *Molothrus ater*	B3, M3	ss
Northern Oriole, *Icterus galbula*	S3, M3	d
Fringillidae		
Rosy Finch, *Leucosticte arctoa*	M5, W5	ss
House Finch, *Carpodacus mexicanus*	S3, M3	f, d
Pine Siskin, *Carduelis pinus*	S5, M3	f, d
American Goldfinch, *C. tristis*	M5	d, ss
Evening Grosbeak, *Coccothraustes vespertinus*	S5, M3	d
Passeridae		
House Sparrow, *Passer domesticus*	B2, M1, W3	f, d

[1] Abundance code (see text for definitions of terms):
1. Abundant
2. Common
3. Uncommon
4. Occasional or local
5. Rare
6. Vagrant or accidental

[2] Breeding and seasonal code:
R = Breeder and year-round resident
B = Summer breeder
M = Migrant
W = Winter visitor
S = Summer visitor; no breeding records

[3] Habitat code (multiple habitats listed for a particular species are given in descending order of preference):
w = on or near water
ss = shrub-steppe
d = deciduous or riparian
j = juniper woodland
g = grassland
sw = sitewide
f = facility complexes

[4] Audubon Blue List (Tate and Tate 1982)

[5] Sensitive Species (USDI Bureau of Land Management)

[6] Endangered (Federal Register 1976)

[7] Species of Special Concern (Idaho Department of Fish and Game, 1977)

TABLE 4. Mammals recorded on the Idaho National Environmental Research Park.

Taxa	Distribution and Habitat	Abundance[1]
INSECTIVORA		
Soricidae		
Merriam Shrew, *Sorex merriami*	Sitewide; sagebrush-steppe	Uncommon
CHIROPTERA		
Vespertilionidae		
Little Brown Myotis, *Myotis lucifugus*	Sitewide; roosts in buildings	Common
Small-footed Myotis, *M. leibii*	Sitewide; rocky outcrops & lava	Abundant
Long-eared Myotis, *M. evotis*	SE NERP; junipers	Common
Big-brown Bat, *Eptesicus fuscus*	Sitewide; roosts in buildings & caves	Common
Hoary Bat, *Lasiurus cinereus*	Patchy; riparian & junipers	Uncommon
Townsend's Big-eared Bat, *Plecotus townsendii*	Sitewide; caves & lava tubes	Abundant
LAGOMORPHA		
Leporidae		
White-tailed Jackrabbit, *Lepus townsendii*	Sitewide; sagebrush-steppe	Occasional
Black-tailed Jackrabbit, *L. californicus*	Sitewide; sagebrush-steppe	Abundant-occasional (cyclic)
Nuttall's Cottontail, *Sylvilagus nuttallii*	Sitewide; sagebrush-steppe, facilities	Common
Pygmy Rabbit, *S. idahoensis*[2]	Patchy; sagebrush-steppe & rocky outcrops	Common
RODENTIA		
Sciuridae		
Least Chipmunk, *Tamias minimus*	Sitewide; sagebrush-steppe	Abundant
Yellow-bellied Marmot, *Marmota flaviventris*	Sitewide; rocky outcrops	Uncommon
Townsend's Ground Squirrel, *Spermophilus townsendii*	Sitewide; sagebrush-steppe, facilities	Common
Geomyidae		
Northern Pocket Gopher, *Thomomys talpoides*	Patchy; sagebrush-steppe	Occasional
Heteromyidae		
Great Basin Pocket Mouse, *Perognathus parvus*	Sitewide; sagebrush-steppe	Uncommon
Ord's Kangaroo Rat, *Dipodomys ordii*	Sitewide; sagebrush-steppe & grassland	Common
Castoridae		
Beaver, *Castor canadensis*	Patchy; Big Lost River	Local
Cricetidae		
Western Harvest Mouse, *Reithrodontomys megalotis*	Sitewide; sagebrush-steppe & grassland	Common
Deer Mouse, *Peromyscus maniculatus*	Sitewide; all habitats	Abundant
Northern Grasshopper Mouse, *Onychomys leucogaster*	Sitewide; sagebrush-steppe	Occasional
Bushy-tailed Woodrat, *Neotoma cinerea*	Sitewide; rocky outcrops	Common
Montane Vole, *Microtus montanus*	Sitewide; grassland & facilities	Abundant-occasional (cyclic)
Sagebrush Vole, *Lagurus curtatus*[3]	Patchy; sagebrush-steppe	Uncommon
Muskrat, *Ondatra zibethicus*	Patchy; aquatic	Rare
Muridae		
Norw, facilities	Common	
poides	Patchy; sagebrush-steppe	Occasional
idae		
in Pocket Mouse, *Perognathus parvus*	Sitewide; sagebrush-steppe	Uncommon
CARNIVORA		
Canidae		
Coyote, *Canis latrans*	Sitewide; all habitats	Common
Mustelidae		
Long-tailed Weasel, *Mustela frenata*	Sitewide; sagebrush-steppe	Common
Badger, *Taxidea taxus*	Sitewide; all habitats	Uncommon
Western Spotted Skunk, *Spilogale gracilis*	Sitewide; rocky outcrops	Rare
Felidae		
Mountain Lion, *Felis concolor*	Sitewide; transient	Vagrant
Bobcat, *F. rufus*	Sitewide; sagebrush-steppe, juniper	Uncommon

Table 4 continued.

Taxa	Distribution and Habitat	Abundance[1]
ARTIODACTYLA		
Cervidae		
Wapiti, *Cervus elaphus*	Sitewide; transient	Vagrant
Mule Deer, *Odocoileus hemionus*	Sitewide; sagebrush-steppe, grassland	Uncommon
Moose, *Alces alces*	Sitewide; transient	Vagrant
Antilocapridae[4]		
Pronghorn, *Antilocapra americana*	Sitewide; sagebrush-steppe, facilities	Abundant
Bovidae		
Mountain Sheep, *Ovis canadensis*	North NERP; transient	Vagrant

[1] See text for definition of abundance terms.
[2] Green and Flinders (1980) place this in the genus *Brachylagus*.
[3] Carleton and Musser (1984) place this in the genus *Lemmiscus*.
[4] O'Gara and Matson (1975) do not recognize Antilocapridae as a valid family and place pronghorn in the family Bovidae.

dominates the area. Winter hibernacula for several species of snakes have been located and described (Sehman 1977). With the exception of the rubber boa, none of the reptiles recorded on the NERP were unexpected. Two species that were expected but not recorded on the Idaho NERP were the leopard frog (*Rana pipiens*) and the western racer (*Coluber constrictor*). Both have been collected within a few kilometers of the site (Sehman and Linder 1978). With the possible exception of these two species, and the possibility of minor range extensions or the discovery of some species in different habitats, the inventory of the herpetofauna on the Idaho NERP is probably complete.

A total of 164 species of birds were recorded on the Idaho NERP (Table 3). One hundred thirty-five species were recorded during the summer months, but only 59 (49%) of these were reported breeding on the site. Emberizids (mostly sparrows and blackbirds), raptors, waterfowl, and swallows accounted for nearly 50% of the breeding species. Breeding records were lacking for 76 species classified as summer visitors. Most of these were waterfowl, shorebirds, and emberizids (mostly warblers and sparrows) with 13, 15, and 15 species, respectively. Forty-six bird species were recorded on site during the winter. Forty of these were also observed on the NERP during the summer. Six species were recorded during the winter only or during the winter and migration. Nineteen species (mostly shorebirds and emberizids) were observed only during migration.

Thirty percent of the wintering species recorded on the NERP were raptors. The number of birds of prey wintering on the NERP is tightly coupled to fluctuations in the black-tailed jackrabbit (*Lepus californicus*) population (Craig et al. 1983). During winters of low jackrabbit abundance (i.e., 1974–75 and 1975–76), an average of fewer than 15 raptors were recorded biweekly along a 187 km survey route. Eighty percent of these were Rough-legged Hawks (*Buteo lagopus*). During the winter of 1981–82, when the rabbit population was high, each survey along the same route averaged nearly 142 raptors. Rough-legged Hawks and Golden Eagles (*Aquila chrysaetos*) accounted for 48% and 30% of the sightings, respectively. As many as 108 Golden Eagles and 15 Bald Eagles have been observed on the NERP in a single day (Watson 1984).

Five species of gallinaceous birds were recorded on the NERP. The Sage Grouse (*Centrocercus urophasianus*) was, however, the only common upland game bird on the park (Table 3). The NERP supports both wintering and breeding populations of Sage Grouse (Connelly 1982, Connelly and Markham 1983, Gates 1983). Wintering flocks include birds that are year-round site residents and large numbers of grouse that summer in the mountain valleys and agricultural areas adjacent to the NERP (Connelly 1982). Sixty-seven sage grouse leks have been identified on the site (Connelly and Ball 1983).

Trost et al. (1977) listed 305 bird species in southeast Idaho. Of these, 216 occur in habitats similar to those found on the Idaho NERP. Thus, the avifauna records presented here represent about 75% of the species that potentially could occur on the Idaho NERP.

Increased efforts, especially during the breeding season, are needed to completely inventory the NERP avifauna.

Thirty-nine species of mammals were recorded on the Idaho NERP (Table 4). With the exception of a few transient species (i.e., moose, *[Alces alces]*, wapiti *[Cervus elaphus]*, mountain sheep *[Ovis canadensis]*, and mountain lion *[Felis concolor]*), the majority of the species were resident on the NERP throughout the year. Most chiropterans presumably migrate from the NERP in the winter, but some of the many caves and lava tubes present on site are used as winter hibernacula. The extent of the wintering bat population is currently under investigation.

Several predator-prey (Johnson 1978, Johnson and Hansen 1979, Laundré et al. 1978, MacCracken 1980, MacCracken and Hansen 1982), synecology (Fraley et al. 1982, Gates 1983, R. Johnson 1982), and autecology (Fisher 1979, French et al. 1965, Grant 1983, Wilde 1978) studies conducted on the Idaho NERP addressed rabbits and hares. Although all leporid populations may be cyclic, numbers of black-tailed jackrabbits were the most variable of the four species found on the NERP. Their densities ranged from less than 0.5/km^2 during population lows to more than 142/km^2 during the peak phase of the cycle (Stoddart 1983). All four leporids occurred sitewide, but the pygmy rabbit (*Sylvilagus idahoensis*) appeared to be most specific in its habitat preference (Wilde 1978).

Many studies on the NERP directly or indirectly addressed rodent populations (e.g., Allred 1973, Groves 1981, Groves and Keller 1983, Halford 1981, Halford and Markham 1978, M. Johnson 1982, Johnson and Keller 1983, Reynolds 1980). Seventeen species representing seven families were recorded on site (Table 4). No rodent species were particularly novel in their presence or conspicuous in their absence on the Idaho NERP. Most rodents were recorded throughout the research park. The montane vole (*Microtus montanus*) and the western harvest mouse (*Reithrodontomys megalotis*) preferred grassland habitat. Predictably, the porcupine (*Erythizon dorsatum*), beaver (*Castor canadensis*), and muskrat (*Ondatra zibethicus*) were most abundant along the Big Lost River, although the latter was occasionally recorded in settling ponds near facilities and, even less frequently, in sagebrush habitat and agricultural fields.

Six species of carnivores were recorded on the NERP (Table 4). Striped skunks (*Mephitis mephitis*) were recorded within 10 km of the southern and southwestern boundary of the site but to date have not been reported on the NERP. With the exception of the spotted skunk (*Spilogale gracilis*), all occurred throughout the site. Coyotes (*Canis latrans*) and weasels (*Mustela frenata*) were the most abundant mammalian predators. Coyotes on the NERP were the focus of several completed and ongoing studies (e.g., Davison 1980, Johnson 1978, Laundré 1979, Stoddart 1983, Woodruff 1977). Two studies have directly addressed bobcats (Bailey 1972, Knick and Ball 1983). Populations of both species track but lag behind cyclic jackrabbit populations. Studies on the other carnivores of the park are lacking.

Pronghorn antelope (*Antilocapra americana*) were the most abundant and conspicuous of the big game animals on the research park. Populations of pronghorn fluctuate seasonally (Hoskinson and Tester 1980, Reynolds and Rose 1978, 1982). More than 4,500 pronghorn were recorded on the park during the winter of 1977–78. During typical summers, about 750 pronghorn used the research park. Little information was available on the mule deer (*Odocoileus hemionus*) of the NERP. Deer were infrequently observed by NERP biologists and other site personnel. Onsite population densities, seasonal movements, and local habitat preferences have not been studied in detail.

No fishes, amphibians, reptiles, or mammals recorded on the Idaho NERP were classified as threatened or endangered species (U.S. Fish and Wildlife Service 1982). However, both the endangered Peregrine Falcon and Bald Eagle were recorded on the NERP. Sightings of the former were rare during all seasons. The Bald Eagle was a consistent, albeit infrequent, winter visitor to the research park.

Although most of the mammals and herpetofauna were recorded throughout the site, less than 30% of the bird species were registered either in shrub-steppe habitat or sitewide in occurrence. Alternatively, on or near water was recorded as the preferred habitat for nearly 40% of the avifauna. Only two species (Clark's Nutcracker [*Nucifraga columbiana*] and Northern Mockingbird [*Mimus polyglottos*]) were recorded in the juniper stands only. Blue Grouse (*Dendragapus obscurus*) and American Redstart (*Setophaga ruticilla*), both accidental species, were the only birds recorded around facilities only.

Although all habitats were not used by wildlife in direct proportion to their availability, all habitats in the park evidently contribute somewhat to the overall diversity of vertebrate species on the NERP. The Idaho NERP provides a protected environment for an unexpected diversity and density of resident and migrant vertebrate species representative of the Snake River Plain and Northern Great Basin ecosystem. Undoubtedly the large expanse of the Idaho National Environmental Research Park, the controlled access requirements, and the relatively undisturbed native habitat are major factors that attract large wintering populations of pronghorn, raptors, and Sage Grouse. Although many ecological studies have been completed on the site since its NERP designation, continued study is required to fully inventory some taxa and to answer some population and distribution questions about others.

ACKNOWLEDGMENTS

We thank J. E. Anderson, H. W. Browers, T. H. Craig, E. H. Craig, G. Devoe, R. J. Gates, D. L. Genter, J. C. Grant, C. R. Groves, M. K. Johnson, B. L. Keller, S. T. Knick, J. G. MacCracken, R. S. McCarty, K. L. Peterson, L. R. Powers, C. H. Trost, and J. W. Watson for aid in preparation of this species list. O. D. Markham, B. L. Keller, and K. S. Moor provided critical reviews of various drafts of the manuscript. This is a contribution of the Idaho National Engineering Laboratory Radioecology and Ecology Programs, funded by the Office of Health and Environmental Research, U. S. Department of Energy.

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INFECTION OF YOUNG DOUGLAS-FIRS AND SPRUCES BY DWARF MISTLETOES IN THE SOUTHWEST

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ABSTRACT.—Mistletoe infection of Douglas-fir and spruce seedlings increased as the mean dwarf mistletoe rating of the overstory, seedling density, and total age of seedlings increased. Percent of spruce seedlings infected increased more rapidly than for Douglas-fir as overstory dwarf mistletoe ratings increased. However, the intensity of infection as measured by the mean dwarf mistletoe rating of seedlings, increased at about the same rate for spruce and Douglas-fir. Percent infection of seedlings less than 20 years total age was higher for spruce than for Douglas-fir. Douglas-fir and spruce seedling mortality was from two to three times greater in heavily infested stands than in healthy stands.

Dwarf mistletoes (*Arceuthobium* spp.) are the most serious disease agent in southwestern mixed conifer forests (Jones 1974). These parasitic flowering plants reduce the growth of heavily infected trees, cause increased mortality, reduce cone and seed production, and may predispose trees to other diseases and insects (Hawksworth and Wiens 1972). The most prevalent and damaging dwarf mistletoe, *A. douglasii* Engelm. It occurs throughout the range of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in the Southwest. Andrews and Daniels (1960) estimated that approximately 50% of the Southwest's Douglas-fir type was infested with Douglas-fir dwarf mistletoe. Another damaging dwarf mistletoe in southwestern forests is the western spruce dwarf mistletoe, *Arceuthobium microcarpum* (Engelm.) Hawksw. & Wiens. It parasitizes Engelmann and blue spruce (*Picea engelmannii* Parry and *P. pungens* Engelm.) in several locations in Arizona, but it is only known from the Mogollon and Sacramento mountains in New Mexico (Hawksworth and Graham 1963a, Hawksworth and Wiens 1972, Mathiasen and Jones 1983). Western spruce dwarf mistletoe is most prevalent in the Apache-Sitgreaves National Forest, Arizona, where it is a primary factor associated with mortality in infested spruce stands (Hawksworth and Graham 1963a).

Douglas-fir and spruce are the most prevalent and commercially important species in southwestern mixed conifer forests. Douglas-fir and spruce regeneration is frequently abundant in the understory of mixed conifer stands in the Southwest (Moir and Ludwig 1979, Gottfried and Embry 1977). When overstories are infested with dwarf mistletoes, spread to young regeneration perpetuates the infestation. Management of mixed conifer forests infested with dwarf mistletoes should minimize the spread of the disease from an infested overstory to the understory and particularly to young regeneration (Jones 1974, Gottfried and Embry 1977).

There are several factors that influence infection of regeneration. Natural infection of seedlings is not common because they represent a relatively small target area for mistletoe seeds (Hawksworth 1958, 1961, Wicker and Shaw 1967), and several factors remove seeds from seedlings (Wicker 1965, 1967). Scharpf (1969) reported that only 7% of true fir seedlings less than three feet tall were infected in heavily infested stands and that infection intensified rapidly in regeneration taller than three feet.

The duration of exposure to inoculum is an important factor influencing seedling infection. Hawksworth (1958) found there is little infection in lodgepole pine (*Pinus contorta* Dougl. ex Loud.) stands less than 15 years old. Hawksworth and Graham (1963b) reported infection of lodgepole pine as young as 6 years in the intermountain region and 8 years in the central Rocky Mountains. Weir (1918) reported the average age of 50 naturally infected Douglas-fir seedlings, used for assessing the effects of dwarf mistletoe on seedling growth, was 18 years, but he did not report the youngest age for the seedlings. Infection of ponderosa pine (*Pinus ponderosa* Laws.) by southwestern dwarf mistletoe (*Arceuthobium vaginatum* subsp. *cryptopodum* (Engelm.) Hawksw. & Wiens) has been documented for 10-year-old seedlings (Gill and Hawksworth 1954, Hawksworth 1961).

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Infection of regeneration in dwarf mistletoe–infested stands has important management implications, but information concerning infection of young regeneration is not available for most species growing in southwestern mixed conifer stands. Therefore, this investigation was undertaken to provide data on the infection of young Douglas-fir and spruce seedlings in dwarf mistletoe-infested mixed conifer stands in the Southwest.

Materials and Methods

In 1979, 150 temporary 0.2 acre plots were established in mixed conifer stands in the Apache-Sitgreaves National Forest, Arizona. Of these, 123 were infested with Douglas-fir dwarf mistletoe. For each Douglas-fir greater than 4.5 feet in height, diameter at breast height (dbh) was measured to the nearest 0.1 inch. All remaining trees greater than 4.5 feet in height were measured at dbh to the nearest 2.0 inch. Dwarf mistletoe ratings (Hawks-worth 1977) were recorded for all living trees and for dead trees whenever possible.

The dwarf mistletoe rating system used divided the live crown of a tree into thirds, and each third was rated separately as: 0, no mistletoe infection; 1, less than 50% of the live branches infected; 2, more than 50% of the live branches infected (Hawksworth 1977). The ratings for each third were totaled to obtain a dwarf mistletoe rating (DMR) for the tree. Mean overstory and seedling dwarf mistletoe ratings (DMR) were calculated by adding the DMRs for all live overstory trees (dbh greater than 1.0) and seedlings (dbh 0.1–1.0) in a stand and dividing the total by the number of trees or seedlings. Infection rates were based on the percentage of live trees in a stand or plot with one or more observable mistletoe infections. Infection intensities were based on the DMR of the overstory of seedlings.

During 1980 and 1981, 237 temporary rectangular plots ranging in size from 0.1 to 0.9 acre were established in mixed conifer stands in the Apache-Sitgreaves (96 plots) and Kaibab (12 plots) national forests, Arizona, and in the Carson (47 plots), Lincoln (57 plots), and Santa Fe (25 plots) national forests, New Mexico. Of these, 159 plots were in stands infested with Douglas-fir dwarf mistletoe and 66 of the plots were in stands infested with western spruce dwarf mistletoe. For each live tree over 4.5 feet in height, dbh (nearest 0.1 inch), and DMR were recorded. Dwarf mistletoe ratings were assigned to dead trees, when possible. Data for Douglas-fir and spruce seedlings (dbh 0.1–1.0 inch) in these plots were combined with 1979 data and used to determine seedling infection rates and intensities by 0.5 DMR classes. A total of 6,903 live and 764 dead Douglas-fir seedlings and 1,424 live and 68 dead spruce seedlings were sampled in the 387 plots.

In 64 of the 159 Douglas-fir dwarf mistletoe-infested plots completed in 1980–81, 364 Douglas-fir seedlings (1–4.5 feet in height) were selected, and total age, DMR, height to live crown, and total height were determined for each seedling. In 31 of the 66 plots infested with western spruce dwarf mistletoe, 234 spruce seedlings (147 Engelmann and 87 blue spruce) were selected and data recorded as for Douglas-fir.

Results

Infection of young Douglas-fir.—Per-cent of seedlings infected increased as DMR in the overstory increased (Table 1), reaching 82% in the most heavily infested plots (DMR greater than 4.0). In the most lightly infested plots (DMR 0.1–0.5) only 3% of the seedlings were infected, whereas infection increased to 24% in plots with an overstory DMR of 0.6–1.5 and continued to increase at an average rate of about 15% for each DMR class (Table 1). Seedling DMR also increased as overstory DMR increased.

In plots with an overstory DMR greater than 2.0, seedling mortality (number of dead standing seedlings) was from two to three times higher than in the healthy plots (Table 1). Highest mortality (24%) was in the most heavily infested plots. The percentage of dead standing seedlings with dwarf mistletoe was 81% for plots with a DMR of 2.6–3.0 but only 63% in the most heavily infested plots (Table 1).

TABLE 1. Infection of Douglas-fir seedlings by overstory $\overline{\text{DMR}}$ classes

Overstory $\overline{\text{DMR}}$	Total number seedlings	Seedling $\overline{\text{DMR}}$	Percent dead	Percent live infected	Percent dead infected
0	1,880	0	7	0	0
0.1–0.5	1,370	0.1	10	3	6
0.6–1.0	504	0.5	9	24	24
1.1–1.5	1,614	0.5	5	24	39
1.6–2.0	646	0.6	9	35	37
2.1–2.5	432	1.0	13	44	46
2.6–3.0	470	1.2	21	56	81
3.1–3.5	288	1.8	14	58	88
3.6–4.0	294	2.1	23	67	71
4.0 +	169	2.8	24	82	63
All seedlings	7,667	0.5	10	22	41

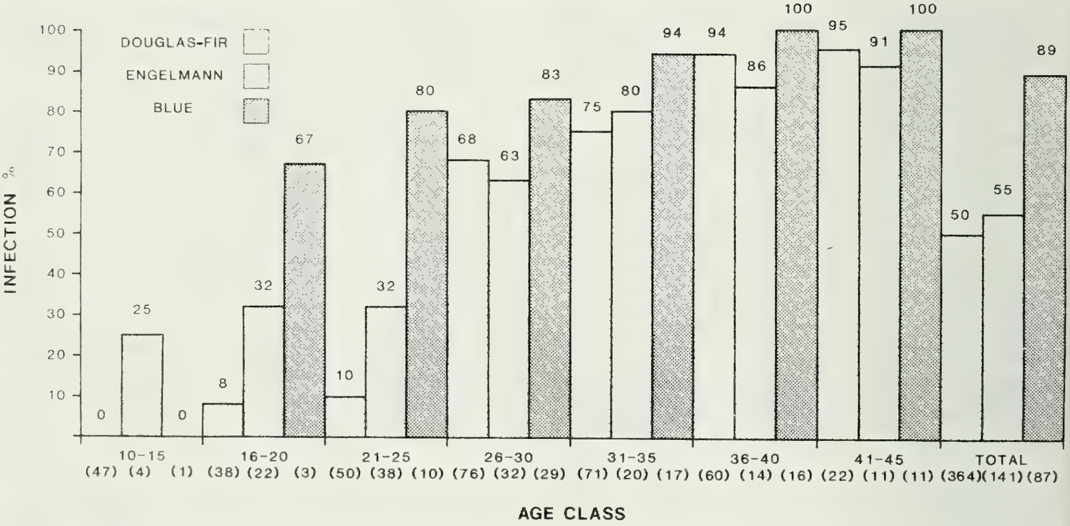

Fig. 1. Infection of Douglas-fir, Engelmann spruce, and blue spruce seedlings by five-year base age classes. Number of seedlings sampled in parentheses.

Infection of seedlings less than 26 years old was low (10% or less), but it was 68% for seedlings 26–30 years old (Fig. 1). Over 90% of the Douglas-fir seedlings greater than 36 years old were infected. Only 3 seedlings less than 20 years old were infected (8%) and these seedlings were in heavily infested stands. Five seedlings that were from 21 to 25 years old were infected (10%).

Infection of Douglas-fir seedlings increased as overstory DMR and seedling density increased (Table 2). Little infection occurred in plots with a DMR less than 1.1 and seedling densities less than 50 per acre. Seedling infection exceeded 50% when the overstory DMR reached 2.1 and seedling density was greater than 50 per acre. From 90% to 100% infection occurred when the overstory DMR exceeded 3.0 and seedling densities were greater than 100 per acre.

INFECTION OF YOUNG SPRUCE.—Percent of spruce seedlings infected increased as overstory DMR increased more rapidly than for Douglas-fir seedlings (Table 3). However, the intensity of infection (seedling $\overline{\text{DMR}}$) increased at about the same rate as for Douglas-fir.

Seedling mortality was approximately twice that of the healthy plots in plots with an overstory DMR greater than 3.0 (Table 3).

Infection of Engelmann and blue spruce were analyzed separately. Infection of both

TABLE 2. Percent infection of Douglas-fir seedlings by overstory $\overline{\text{DMR}}$ classes and seedling density classes.

	Overstory $\overline{\text{DMR}}$ Class								
Seedlings per acre	0.1–0.5	0.6–1.0	1.1–1.5	1.6–2.0	2.1–2.5	2.6–3.0	3.1–3.5	3.6–4.0	4.0 +
	Percent Infection								
Less than 25	0	0	9	12	25	33	45	57	76
25– 50	0	10	19	39	42	58	66	79	84
51– 75	0	22	18	30	51	64	74	93	94
76–100	3	14	28	41	39	69	76	95	100
101–125	5	12	26	30	60	60	83	100	100
126–150	7	17	29	36	89	87	95	—	—
More than 150	10	30	35	60	70	89	—	—	—

–No sample

species was not different until an overstory DMR class of 1.6–2.0 was reached, after which infection of blue spruce was greater than for Engelmann spruce (Tables 4 and 5). However, the intensity of infection, as indicated by seedling DMR, for blue spruce was much greater in most DMR classes (the lightest and most heavily infested plots were similar). Mortality in the infested plots for both species varied greatly by DMR class. Past infection of dead seedlings was high for both species (Tables 4 and 5).

Percent infection of young spruce seedlings (less than 20 years) was higher than for Douglas-fir (Fig. 1). However, percent infection in the older age classes was nearly the same as for Douglas-fir. The sample size for blue spruce seedling infection in the first three age classes is too small to be compared with Engelmann spruce. Infection remained greater for blue spruce in the older age classes, but again sample sizes are small.

DISCUSSION

Wicker (1965) discussed the many factors influencing natural infection of seedlings by dwarf mistletoes and provided data on the influence of seedling target area. This investigation provides additional data on the influence of three of the factors listed by Wicker: length of time seedlings are exposed to inoculum (total age of seedlings), amount of inoculum (as expressed by overstory DMR), and density of seedlings (as expressed by seedlings per acre). Information on these factors has important management implications in minimizing infection of young regeneration in southwestern mixed conifer stands.

Despite the relatively small target areas and exposure times represented by seedlings, nearly one-fourth of the Douglas-fir seedlings in the lightly infested stands sampled (DMR 0.1–1.5) were infected. Infection of spruce seedlings was even greater. Infection rate and intensity of blue spruce seedlings increases more rapidly than for Engelmann spruce. This could be due to differences in susceptibility to western spruce dwarf mistletoe between these species or to differences in seedling characteristics, such as foliage retention or greater crown ratios, for blue spruce.

Very young Douglas-fir seedlings are rarely infected in Douglas-fir dwarf mistletoe-infested southwestern mixed conifer stands. Only 6% of the Douglas-fir seedlings sampled that were less than 26 years old were infected, whereas infection of older seedlings averaged 83%. Infection of Douglas-fir seedlings less than 26 years old is primarily related to one or more of the following seedling or stand characteristics:

1. Seedling density–Young seedlings in stands with high seedling densities in the understory (greater than 100 seedlings per acre) have more total available target area for seed capture.
2. High inoculum potential–Stands with young infected seedlings had moderately to heavily infested overstories. (DMR greater than 2.0).
3. Seedling age–Older seedlings have been exposed to inoculum sources for a longer period.

When regeneration is heavy, even low levels of infection in the overstory can cause high rates of Douglas-fir seedling infection. Infec-

TABLE 3. Infection of Engelmann and blue spruce seedlings by overstory $\overline{\text{DMR}}$ classes.

Overstory $\overline{\text{DMR}}$	Total number seedlings	Seedling $\overline{\text{DMR}}$	Percent dead	Percent live infected	Percent dead infected
0	621	0	5	0	0
0.1–0.5	106	0.1	1	10	100
0.6–1.0	44	0.5	10	30	50
1.1–1.5	193	0.6	2	39	67
1.6–2.0	171	0.8	2	54	100
2.1–2.5	125	1.1	7	61	75
2.6–3.0	127	1.4	5	76	100
3.1–3.5	17	1.9	13	90	100
3.6–4.0	80	3.0	11	92	100
4.0 +	8	3.0	14	100	0
All seedlings	1,492	0.6	5	31	46

tion of Douglas-fir seedlings greatly increases after they reach ages greater than 25 years.

Spruce seedlings are infected more frequently than Douglas-fir seedlings and at younger ages. Of all spruce seedlings sampled that were less than 26 years old, 39% were infected. Average infection of older spruce seedlings was approximately the same as for Douglas-fir (83%). It appears as though the probability of infection of young spruce seedlings (less than 10 years) is higher than for Douglas-fir, but more data are needed. As for Douglas-fir, the probability of infection of spruce seedlings older than 30 years in dwarf mistletoe-infested mixed conifer stands is relatively high.

Of the spruce seedlings sampled that were less than 21 years old, 33% were infected. The same seedling or stand characteristics that contribute to infection of young Douglas-fir seedlings affect the infection of young spruce seedlings. Because young spruce seedlings are infected more frequently than Douglas-fir and at younger ages, infection of spruce seedlings in stands with low seedling densities and lower levels of overstory infection can be high also.

Another factor of importance to management of moderately to heavily infested stands is increased Douglas-fir seedling mortality caused by Douglas-fir dwarf mistletoe. Seedling mortality in these stands is from two to three times greater than in healthy or lightly infested stands. Because a high percentage of these dead seedlings had been infected, it is probable that mistletoe infection contributed to the increased mortality. Several investigators have demonstrated that dwarf mistletoes severely affect seedling growth (Weir 1918, Roth 1971, Knutson and Toevs 1972, Knutson 1974), but little information is available on what levels of mistletoe infection cause seedling mortality under natural conditions and how this process varies between species and under different stand conditions. Increased seedling mortality in Douglas-fir dwarf mistletoe-infested stands is evident from this study, and this type of damage contributes to the lower overall production potential of dwarf mistletoe-infested mixed conifer stands.

Spruce seedling mortality did not increase beyond the levels found in healthy stands until stands were heavily infested (overstory $\overline{\text{DMR}}$ greater than 3.0). This may indicate that spruce seedlings are capable of tolerating higher infection intensities than Douglas-fir. However, the sample size for spuce seedlings in the most heavily infested plots was small, and more data on the relationships between stand infestation intensity and spruce seedling mortality are needed.

Dwarf mistletoes are the most damaging and prevalent disease agents in southwestern mixed conifer forests, and silvicultural management plans that do not successfully prevent or reduce infection of young regeneration only perpetuate the problems that now exist in many of these stands. Cutting cycles of 20 years or less with intermediate sanitation removals in dwarf mistletoe-infested stands can effectively reduce the amount of damage in the present stand as well as significantly reduce infection of new and established regeneration.

TABLE 4. Infection of blue spruce seedlings by overstory $\overline{\text{DMR}}$ classes.

Overstory $\overline{\text{DMR}}$	Total number seedlings	Seedling $\overline{\text{DMR}}$	Percent dead	Percent live infected	Percent dead infected
0	460	0	6	0	0
0.1–0.5	82	0.1	0	10	0
0.6–1.0	7	1.0	17	33	0
1.1–1.5	49	0.9	4	43	50
1.6–2.0	33	1.2	0	61	0
2.1–2.5	42	1.5	5	78	50
2.6–3.0	63	2.1	9	95	100
3.1–3.5	10	2.3	0	90	0
3.6–4.0	78	3.0	11	91	100
4.0 +	8	3.0	14	100	0
All seedlings	832	0.7	6	28	35

TABLE 5. Infection of Engelmann spruce seedlings by overstory $\overline{\text{DMR}}$ classes.

Overstory $\overline{\text{DMR}}$	Total number seedlings	Seedling $\overline{\text{DMR}}$	Percent dead	Percent live infected	Percent dead infected
0	161	0	3	0	0
0.1–0.5	24	0.1	4	9	100
0.6–1.0	37	0.4	9	29	33
1.1–1.5	144	0.5	1	38	100
1.6–2.0	138	0.7	3	52	100
2.1–2.5	83	0.9	8	52	83
2.6–3.0	64	0.9	2	59	100
3.1–3.5	7	1.2	40	60	100
3.6–4.0	2	3.0	0	100	0
4.0 +	—	—	—	—	—
All seedlings	660	0.5	3	34	68

—No sample

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HABITAT RELATIONSHIPS OF SALTCEDAR (*TAMARIX RAMOSISSIMA*) IN CENTRAL UTAH

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ABSTRACT.—Nineteen study sites were established in areas infested with saltcedar bordering Utah Lake in central Utah. Saltcedar cover on the sites averaged 57% but varied widely from community to community. Seventeen soil factors were measured relative to the stands studied. Cover of saltcedar was regressed against the different soil factors, but no patterns were detected. Saltcedar functioned equally well at all levels of each gradient studied and appeared able to accommodate wide variations in all factors studied. It is suggested that saltcedar has evolved a general-purpose genotype that contributes to its being a vigorous and troublesome weed. Criteria as to why it is such an aggressive weed are listed.

Saltcedar (*Tamarix ramosissima*) is an important introduced shrub and phreatophyte in western North America, where it occupies vast acreages. Saltcedar is a vigorous woody invader of moist pastures, rangelands, and riparian habitats. It is poor in forage value, and as a weed it continually causes management problems.

The genus *Tamarix* is native to the Mediterranean area. It is one of four genera of the Tamaricaceae common in Africa, Europe, and Asia. For a time it was thought that species of Tamarix were brought to the Americas by Spanish explorers. However, since the only early sightings of saltcedar were along the U.S.-Mexican border, it appears that such may not be the case (Robinson 1965). It is now believed that the first introduction of saltcedar to North America was made by nurserymen on the east coast of the United States in 1823. According to Horton (1964), saltcedar was offered for sale that year by the Old American Nursery operated by Lawrence and Mills. Later, in 1828, Bartram's nursery of Philadelphia was selling saltcedar. When in 1868 the U.S. Department of Agriculture began raising saltcedar, it reported six different species growing in the Department Arboretum (Horton 1964).

Saltcedar made its appearance on the West Coast of the United States in the 1850s. Several California nurseries offered two or three species for sale as early as 1854 (Robinson 1965). It is believed that these western nurseries were supplied by those in the East.

Although saltcedar was planted as an ornamental in the western United States during the latter half of the 1800s, it apparently did not escape cultivation until the 1870s. The only accurate information concerning sightings is found in herbarium collections. The earliest collection of saltcedar (*T. gallica*) was in 1877 near Galveston, Texas. Thereafter, sightings were reported in Arizona, California, New Mexico, and Utah (Robinson 1965).

For the next several decades, little attention was paid to the increasing spread of saltcedar, and there is no record that anyone was aware that a problem was in the making. For example, in the early 1900s farmers were using this plant for erosion control (Everitt 1980). However, it became clear by the 1920s that saltcedar was becoming a serious problem. By then saltcedar was spreading rapidly from one watershed to another. It spread up and down nearly every stream in the Southwest, and then northward into the Great Basin and the Rocky Mountains.

Fathers Dominguez and Velez de Escalante, on their expedition to Utah Valley in 1776, described lush pastures, willows, alders and poplar trees, but they made no mention of saltcedar (Auerbach 1943). The first report of saltcedar in Utah was from St. George in the 1880s, where it was grown as a cultivated species (Robinson 1965). M. E. Jones collected specimens at Harrisburg and Silver Reef, Utah, in 1894 (Robinson 1965). The next reported sightings were by Walter Cottam

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(1926), when he identified saltcedar in his study of the flora of Utah Lake (Cottam 1926). Soon after Cottam's study, Wakefield (1937) stated that *Tamarix* was one of the primary invaders of Utah Lake plant communities between 1930 and 1936. By 1942 Saltcedar had spread to Bird Island in the middle of Utah Lake (Beck 1942). It must have just recently arrived there, however, because it was not mentioned in a study of Bird Island by Hayward in 1935.

Murphy (1951) recorded that saltcedar could be found in all the shore communities surrounding the lake. By the early 1960s concern was being expressed over the saltcedar invasion, particularly by Christensen (1962). He wrote that "Tamarix occurred as a major species along much of the lake shore, and that [sic] dense stands of Tamarix plants one, two or three years old, [sic] were a conspicuous feature of the vegetation on the recently exposed beaches." By 1962 saltcedar was actively invading not only the lower valley streams and lakes, but those in the mountains as well. Christensen (1962) mentioned sightings of saltcedar in Spanish Fork Canyon along the Spanish Fork River at elevations between 4,900 and 5,000 feet and in Provo Canyon on the shores of Deer Creek Reservoir at elevations of 5,400 feet. More recent descriptions of the saltcedar communities surrounding Utah Lake are by Coombs (1970) and Brotherson and Evenson (1982).

Brotherson and Evenson (1982) described the aerial extent and densities of saltcedar communities surrounding Utah Lake. They concluded that saltcedar now occupies about 2,000 acres, or 3.7% of the total land area close to the lake. Furthermore, they suggested that additional invasion is likely.

Although research studies concerning saltcedar invasion and its eradication are numerous, few studies have dealt with its physiology and ecology. Everitt (1980) indicated a need for more ecological studies to help determine the relationships of saltcedar to its environment. In this paper we describe the biotic and abiotic factors influencing the saltcedar communities in central Utah.

STUDY AREA

Nineteen study sites were established in June and July of 1980 in saltcedar communities bordering Utah Lake, Utah County, Utah, at approximately 40 degrees 10'N, 11 degrees 50'W (Fig. 1). Elevations at the sites ranged from 1,370 m to 1,402 m.

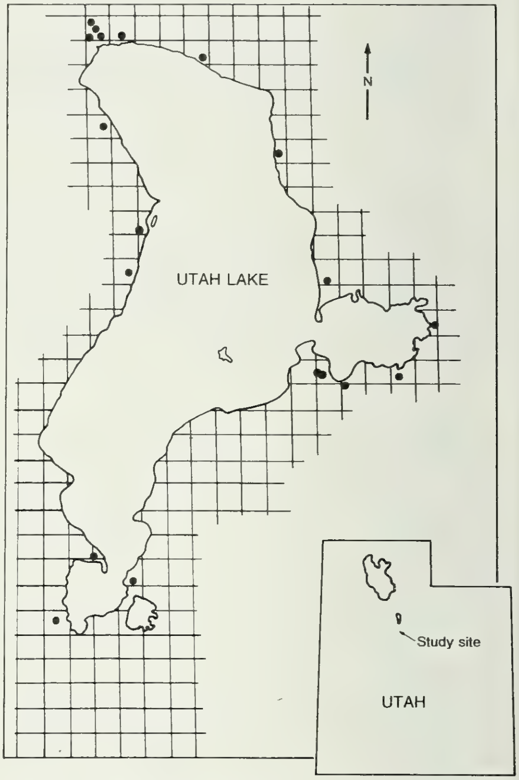

Fig. 1. Map of study site locations in the saltcedar community in central Utah.

Annual precipitation in the area averages 340 mm (14 inches), 60% falling during the winter and spring months. Temperatures range from −13 C to 36 C, July being the hottest month and January the coldest. The majority of water entering Utah Lake comes from streams heading in the Wasatch and Uinta mountains east of the lake. Precipitation in these mountains ranges from 760 to 1,270 mm (30 to 50 inches) annually (Swenson et al. 1972).

MATERIALS AND METHODS

The study sites were selected to represent typical saltcedar communities in the Utah Lake area. A 10 x 10 m study plot was established at each site. Study plot boundaries were marked by a cord 40 m long with loops every 10 m for corners. Each plot was subsampled, with twenty 0.25 m quadrats distributed uniformly across the plot on a 2 x 2 m grid in five rows of four quadrats each.

Total cover of living plants, plant cover by life form (i.e., trees, shrubs, perennial forbs, perennial grasses, sedges, rushes, annual grasses, annual forbs), litter, and bare soil were estimated from each quadrat following a procedure suggested by Ostler (1980). Cover of individual plant species was estimated, using the cover-class categories suggested by Daubenmire (1959). Species were also classified according to whether they were perennial, biennial, or annual, and whether they were native or introduced.

Three soil samples from the top 20 cm of the soil profile were taken in each plot (from opposite corners and the center) and were later combined for laboratory analysis. The soil samples were analyzed for texture (Bouyoucos 1951), pH, soluble salts, mineral composition, and organic matter. Soil reaction was taken with a glass electrode pH meter. Total soluble salts were determined with a Beckman electrical conductivity bridge. A 1:1 q/v soil-water paste (Russell 1948) was used to determine pH and total soluble salts. Soils were extracted with 1.0 neutral normal ammonium acetate for the analysis of exchangeable calcium, magnesium, potassium, and sodium (Jackson 1958, Hesse 1971, Jones 1973). Zinc, manganese, iron, and copper were extracted from the soils by use of DTPA (diethylenetriaminepenta-acetic acid) extracting agent (Lindsay and Norvell 1969). Individual ion concentrations were determined using a Perkin-Elmer Model 403 atomic absorption spectrophotometer (Isaac and Kerber 1971). Soil phosphorus was extracted with sodium bicarbonate (Olsen et al. 1954). Total nitrogen was determined using macro-Kjeldahl procedures (Jackson 1958). Organic matter was determined by methods described by Allison et al. (1965) through weight loss following ignition of a 10 gram soil sample at 950 C in a LECO medium temperature resistance furnace.

The following characteristics were recorded for each plot: elevation (taken from published U.S. Department of Interior Geological Survey 7.5-minute series topographic maps), percent slope, slope position (1 = ridge top, 2 = midslope, 3 = drainage accumulation area), erosion (0 = none, 1 = light, 2 = moderate, 3 = heavy), moisture (1 = dry, 2 = moist, 3 = wet, 4 = seasonally inundated, 5 = submerged), and grazing impact (0 = none, 1 = light, 2 = moderate, 3 = heavy).

Plant nomenclature follows Welsh and Moore (1973) for the dicotyledons (trees, shrubs, forbs, etc.) and Cronquist et al. (1977) for the monocotyledons (grasses, sedges, rushes, etc.). Prevalent species (those most frequently encountered during sampling) of the various plant communities are reported as equal to the average number of species per 0.01 ha sampling area examined (Warner and Harper 1972). Diversity values were computed following Pielou (1977).

Data analysis consisted of computing means, standard deviations, and coefficients of variation for all measured biotic and abiotic variables (Ott 1977). Linear regression analysis (Cochran and Snedecar 1976) was applied to the cover values of saltcedar in relationship to associated soil factors to determine the degree to which they were associated.

Results and Discussion

Saltcedar (*Tamarix ramosissima*) has invaded a wide variety of community types in central Utah since its introduction near the turn of the century. It now occupies a number of disjunct sites totaling nearly 2,000 acres, or about 3.2% of the land area, around Utah Lake and its bays. It forms part of many different communities in the area but is found more often in seasonally submerged sites or saline meadows. In much of the area it forms almost pure stands, and it is the most widespread introduced species around the lake. Its presence represents the invasion of an exotic species into the natural communities, and thus the establishment of a new vegetation type in the area.

There are two vegetation layers in the saltcedar community, the tree-shrub overstory and an herbaceous understory. The herbaceous understory is important in all areas, where it varies greatly from site to site. The variation is in species and in the internal heterogeneity of the vegetation.

Saltcedar is the dominant overstory species, whereas saltgrass (*Distichlis spicata*) is

TABLE 1. Means and standard deviations of prevalent species associated with saltcedar communities around Utah Lake.

Species	Percent presence	Mean frequency	Mean cover	Stand deviation	Coefficient of variation
Tamarix ramosissima	100.0	82.1	56.7	24.1	43.0
Distichlis spicata	79.3	70.5	48.5	35.1	73.0
Kochia scoparia	63.2	31.6	13.5	26.9	198.0
Cardaria draba	15.8	10.8	7.7	22.9	299.0
Iva axillaris	42.1	26.8	6.6	11.0	166.0
Polypogon monspeliensis	68.4	25.3	5.4	9.2	170.0
Cynodon dactylon	5.2	5.2	4.9	21.5	436.0
Atriplex patula	47.4	16.8	4.6	8.9	191.0
Bromus tectorum	26.3	10.5	4.4	15.4	350.0
Hordeum jubatum	36.8	15.5	3.0	7.5	252.0
Poa pratensis	5.2	5.2	2.9	12.7	435.0
Juncus arcticus	26.3	15.0	2.6	5.0	189.0
Lepidium montanum	26.3	12.4	2.3	5.6	244.0

the dominant understory species (Table 1). The compositional patterns of the community seem related to the tendency of saltcedar to invade predominantly saline meadow areas around the lake. The saltcedar community shows some modification by human activities. Coombs (1970) considered the type to be expanding and suggested that much of the saltcedar community was in various stages of recovery from disturbance. If his evaluation is accurate, it appears that this woodland community will undergo a great deal of change in the future.

The saltcedar community around the lake is dominated by trees and perennial grasses; annuals and perennial forbs make smaller but significant contributions. Shrubs, sedges, and rushes contribute only 1%–2% of the total cover (Table 2). Total cover varied little across the study sites, averaging nearly 98%.

Diversity values and species-richness figures varied widely (Table 2). A total of 85 species were encountered on the study sites, but only 13 species were abundant enough to be considered prevalents (Table 1). The 13 prevalent species contributed 85% of the total cover on the study sites, whereas the other 72 species contributed the remaining 15%. Also, the average coefficient of variation ($CV = 236\%$) for the cover values of the individual prevalent species was significantly lower ($p < 0.05$) than the same value ($CV = 370\%$) for the nonprevalents. This indicates that the understory composition of the saltcedar community is highly varied and heterogeneous. The coefficients of variation were high for both prevalent and nonprevalent species, indicating uneven or patchy distribution for all species. In contrast to most species, saltcedar and saltgrass were more abundant and uniformly distributed. This is further evidenced by the percent presence and mean frequency values (Table 1), which are low for all species except saltcedar and saltgrass.

Eight of the 13 prevalent species were introduced. Together they made up 61% of the cover of the prevalent species. The remaining portion of the prevalent species cover was contributed by saltgrass. Thirty-seven species in the community (45%) were introduced. Together these species contributed 56% of the total cover on the study sites (Table 2). Since introduced species generally invade sites of moderate to high disturbance, these data support the contention of Coombs (1970) that the saltcedar community occupies areas of high disturbance.

The saltcedar communities in the Utah Lake area occupy sites with intermediate moisture, high water tables, little erosion, and uniform elevations of about 1,386 m (Table 2). Soils were silt loams and silt clay loams high in organic matter with little or no rock in the profile. Soluble salt concentrations in the soils ranged from 650 to 16,000 ppm and averaged 5,994 ppm. In an earlier study Carmen and Brotherson (1980) showed that differences in soil salt concentrations distinguished sites infested by saltcedar from adjacent uninfested sites and from sites infested by Russian Olive (*Elaeagnus angustifolia*). The high level of salts, along with basic

TABLE 2. Highs, lows, range, means, and standard deviations and coefficients of variation for environmental factors (biotic and abiotic) for saltcedar community around Utah Lake. (a) The slope position is defined as 1 = top of ridge, 2 = midslope, 3 = bottom of slope. (b) The moisture index runs from 1 to 5, with 1 indicating xeric conditions and 5 indicating standing water. (c) Grazing impact is defined as 1 = light, 2 = moderate, 3 = heavy grazing.

Environmental factor	High	Low	Range	Mean	Standard deviation	Coefficient of variation
GENERAL SITE FACTORS						
Elevation	1399.9	1368.6	31.4	1386.1	9.5	1.0
Slope position	3.0	1.0	2.0	2.0	1.0	50.0
Moisture	3.0	1.0	2.0	2.3	0.7	29.0
Percent litter cover	5.8	0.0	5.8	0.5	1.3	290.0
Percent exposed bareground	5.6	0.0	5.6	1.7	3.2	189.0
GENERAL SOIL FACTORS						
Percent sand	73.0	14.0	59.0	32.8	14.9	45.0
Percent silt	70.0	17.0	53.0	44.8	16.1	36.0
Percent clay	54.0	2.5	51.5	22.4	13.8	62.0
Percent fines	86.0	27.0	59.0	67.2	14.9	22.0
Percent organic matter	20.0	4.2	15.8	10.7	4.6	43.0
pH	9.0	7.0	2.0	8.0	0.5	6.0
Soluble salts (ppm)	16058.0	652.0	15406.0	5994.6	4164.8	69.0
SOIL MINERAL NUTRIENTS						
Nitrogen (percent)	0.7	0.1	0.5	0.3	0.1	42.0
Phosphorus (ppm)	89.6	10.9	78.7	24.9	17.3	70.0
Calcium (ppm)	51120.0	6096.0	45024.0	11736.5	9954.4	85.0
Magnesium (ppm)	2325.0	376.0	1949.0	1325.0	544.4	41.0
Sodium (ppm)	5976.0	235.0	5741.0	2042.7	1526.9	75.0
Potassium (ppm)	1824.0	78.0	1746.0	761.5	429.0	56.0
Iron (ppm)	188.2	3.8	184.4	40.4	45.8	114.0
Manganese (ppm)	41.9	1.6	40.3	13.8	11.3	82.0
Zinc (ppm)	18.6	0.6	18.0	3.8	4.4	114.0
Copper (ppm)	7.6	0.5	7.1	3.1	2.0	66.0
BIOTIC FACTORS						
Total living cover	100.0	94.4	5.4	98.8	1.9	2.0
Percent tree cover	45.0	8.8	36.3	29.5	10.0	34.0
Percent shrub cover	8.0	0.4	7.6	1.2	2.5	208.0
Percent perennial shrub cover	55.0	0.0	55.0	14.1	13.9	99.0
Percent perennial grass cover	61.4	0.0	61.4	32.4	17.7	55.0
Percent sedge cover	8.0	0.0	8.0	1.7	2.7	157.0
Percent rush cover	11.0	0.0	11.0	0.6	2.5	435.0
Percent total annual cover	64.0	0.0	64.0	20.5	19.5	95.0
Percent annual grass cover	58.0	0.0	58.0	7.5	13.8	183.0
Percent annual forb cover	56.0	0.0	56.0	13.0	15.7	121.0
Diversity	3.2	1.0	2.2	2.2	0.5	23.0
Mean no. of species/stand	25.0	5.0	20.0	11.7	5.2	44.0
Mean no. of native species/stand	15.0	2.0	13.0	6.5	3.6	55.0
Mean no. of introduced species/stand	14.0	2.0	12.0	5.3	3.1	59.0
Native species (percent of total)	75.0	26.0	49.0	54.8	14.6	27.0
Introduced species (percent of total)	75.0	25.0	50.0	45.2	14.6	32.0
Total cover of native species	88.0	1.0	87.0	44.1	23.6	54.0
Total cover of introduced species	99.0	12.0	87.0	55.9	23.6	42.0
Grazing impact	3.0	1.0	2.0	2.1	0.7	35.0

pH levels (mean pH = 7.5), indicate a preference by saltcedar for somewhat alkaline substrates.

Soil mineral ion concentrations are shown in Table 2. The soils are characterized by high levels of phosphorus and calcium. All minerals studied appear abundant and are probably not limiting for plant growth. Concentrations for all elements varied widely among sites, with coefficients of variation ranging from 41% to 140%.

When cover of saltcedar was regressed against 17 different soil factors, no patterns were detected. Saltcedar did equally well at all levels of each mineral gradient studied and appeared able to accommodate wide varia-

TABLE 3. Characteristics of saltcedar that contribute to its success as a weed. (*) corresponds to Baker's (1974) criteria of the ideal weed.

*1. Continuous seed production for as long as growing season permits.
*2. Cross-pollination by the wind.
*3. Self-compatible when cross-pollination unavailable.
*4. Very high seed output in favorable environmental circumstances.
*5. Ability to produce some seed under a wide range of environmental conditions.
*6. Adaptations for long or short range dispersal.
*7. A vigorous vegetative reproduction capability.
*8. Brittleness in its stems, and not easily drawn from the ground.
*9. Salt-glands that allow its individuals to compete interspecifically by allelochemics.
10. Tolerance for an extreme range of environmental conditions.
11. Vigorous root sprouter following fire.
12. A "facultative phreatophyte," as distinguished by its ability to live totally inundated or in total absence of saturated soils.
13. Resistance to control with foliar chemicals.

tions in these abiotic factors. It appears, therefore, that the major conditions necessary for saltcedar's success in the Utah Lake environment are alkaline soil conditions, available soil water, and sufficient disturbance of natural vegetative cover to permit the species to become established.

Observations in the field indicated that seedling establishment occurred most often when soils were seasonally saturated at the surface. These findings agree with those of Tomanek and Ziegler (1960), who indicated that the establishment of saltcedar seedlings in the greenhouse depended on high moisture levels at or near the soil surface.

Once established, the primary root of saltcedar grows steadily downward with little branching until it reaches the water table. Secondary branching of the root becomes profuse on contact with the water table (Tomanek and Ziegler 1960). The primary root of a tree in one study (Merkel and Hopkins 1957) was followed to a depth of 16 feet, where it was still 3/16 inch in diameter. At that point the root was still descending. The water table was located at a depth of 26 feet.

Saltcedar has been labeled an "extreme phreatophyte" because of its ability to exploit deep water tables. However, once established, it can survive almost indefinitely in the absence of surface saturation of the soil (Everitt 1980). Because of saltcedar's ability to accommodate such wide variation in its environment, it is often a troublesome weed. Baker (1974) developed a list of characteristics expected in "the ideal weed." At that time he indicated that there were no species that filled all categories; however, the greater the number of weedy characteristics combined in a single species, the more serious a weed the plant should be. Saltcedar as a species combines 9 of his 12 characteristics (Table 3). To Baker's 9 we have added 4 more characteristics (Table 3) that also appear equally important for saltcedar to become a successful and troublesome weed. An important outcome of the incorporation of the listed characteristics, through an "evolutionary synthesis" in saltcedar, has been the development of a general purpose genotype, and thus a vigorous weed capable of exploiting a wide spectrum of habitats.

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CHARACTERISTICS OF MULE DEER BEDS

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ABSTRACT.—Rocky Mountain mule deer (*Odocoileus hemionus hemionus*) beds were studied in selected plant communities with the purpose of characterizing bedding sites. Six trends exist among the data: (1) deer appeared to prefer bedding under or near conifers, (2) most beds were found on or near game trails, (3) beds in xeric communities were located at higher altitudes and had less overhead cover than in mesic communities, (4) the percentage of uphill cover in xeric areas was greater than in mesic areas, (5) visibility was lower on the north and west sides of deer beds in both community types than on the south and east sides, and (6) the mean size of deer beds was the same in both xeric and mesic communities. These trends, as well as other tendencies in bed locations, are considered from the standpoint of deer thermoregulation and predator avoidance.

One essential requirement of wildlife habitat is the covert (King 1938), a place of hiding or concealment, which for mule deer takes the form of a "bed." The purpose of this study was to characterize mule deer beds and bedding sites. Deer beds in central Utah were examined to determine if selected bedding sites provided potential protection from environmental extremes and predators and to consider temporal patterns, types of habitat, and adaptive behavior patterns of mule deer.

Mule deer live in extremely variable environments. Within the Stewart Falls study area of Mt. Timpanogos, daily temperature extremes ranged from −4 to 26 C. According to Linsdale and Tomich (1953), deer bed whenever weather conditions exceed the range of effective thermal homeostasis (Short 1981). They also bed to ruminate. Nevertheless, deer usually tolerate extreme cold better when feeding than when at rest. Many authors report mule deer seek cover when ambient temperature exceeds 15 C, and during winter cold they show a strong preference to bed in areas sheltered from prevailing winds (Miller 1968, 1970, Dasmann and Taber 1956). Many behavioral and anatomical characteristics of mule deer show how important thermoregulatory mechanisms are to cervids. For example, vascularization of the velvet integument that covers growing antlers dissipates body heat (Stonehouse 1968). Most authors agree that deer bed for thermoregulatory or energetic benefit (Darling 1937, Linsdale and Tomich 1953, Stonehouse 1968, Miller 1968, 1970, Short 1981). Flinders and Elliott (1979) showed that, for jackrabbits (*Lepus californicus*), "forms" function as an environmental compromise to aid in regulation of body temperature. The same is true for mule deer that tend to seek cover during periods of extreme ambient temperatures (Short 1981).

Not only are beds selected to protect against environmental extremes, they are chosen to facilitate predator avoidance. The ruminant habit of deer has apparently lead to selection for behavioral responses that permit animals to choose beds where rumination can occur without increasing vulnerability to predators (Geist 1981). Bedding sites exhibit features that permit deer to sense the approach of predators by sight, olfaction, or sonification, and allow for either concealment or escape. Bedding sites are often near cliffs, rocks, or trees, apparently because the approach of predators is hampered from blind sides and the image of the bedded animal is broken up.

Mule deer seem habitually restricted to a home range that consists of a series of small feeding, bedding, watering, and escape areas (Dasmann and Taber 1956). Except during the rut, mature males are segregated from does and fawns. Partitioning of the habitat has placed bucks on more elevated sites, on more exposed south-facing slopes, and in more xeric environments. Females and young occur more frequently in topographical depressions, on densely vegetated north slopes, and in more mesic sites (Dasmann and Taber 1956, Miller 1970, McCullough 1979, King and Smith 1980, Bowyer 1984). Within these respective habitats, it would be advantageous for deer to find bedding sites that afford thermoregulatory and predator-avoidance benefits. The constituent features of various deer beds observed reflect utilization of available topographic and environmental factors and other elements that can be used for their benefit.

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Study Area

Two sites in central Utah were studied. One site was on Mt. Timpanogos in the area of Stewart Falls, Utah County, (3.2 km above Sundance Ski Resort). This is a fairly heterogeneous area with steep, rugged canyons and plentiful springs and streams. Several cliffs and higher elevations of the area are steep and less densely vegetated. Deer inhabitants are part of Utah Deer Herd 15. Elevation ranges from 2,600 to 3,200 m. The lower part of this study area is used extensively by cabin owners and hikers, but no roads penetrate the study area.

The other site was in Eccles Canyon drainage 8 km south of Scofield, Carbon County. The north-facing slope of this canyon is predominantly spruce-fir, with aspen in some of the less declivitous areas. The south-facing slope is mostly xeric, with sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), snowberry (*Symphoricarpos oreophilus*), gambel's oak (*Quercus gambelii*), and other shrubs. Pockets of aspen (*Populus tremuloides*) occur in the draws and on less steep inclines. A perennial stream courses the narrow bottom of Eccles Canyon and the South Fork of Eccles Canyon. A coal mine is presently operating in Eccles Canyon and another is under construction. The gravel road in the bottom of the canyon is heavily traveled by mine personnel and recreationists. Deer inhabiting the area are part of Utah Deer Herd 32. Elevation varies from 2,100 to 2,900 m.

Methods

Deer beds were initially located by randomly walking both study areas. Subsequently, 10 linear transects, 750 m long with 250 m cross transects every 250 m were traversed to detect deer beds. Bedding sites were distinguished as oblong depressions in the soil or as flattened areas of vegetation. Sites were confirmed to be deer beds by the size of the depression, which conforms closely with the size and shape of a deer (Linsdale and Tomich 1953), and by the presence of deer hair, fecal pellets, or deer tracks.

Data collected at each bed site were: (a) habitat type (xeric or mesic), (b) percent cover over the bed and on uphill, downhill, and lateral sides of the bed, (c) position relative to deer trails, (d) vegetation type, (e) size of the bed, (f) percent visibility on north, south, east, and west sides, and (g) slope position. Xeric habitats were defined as those with dry surfaces, primarily facing south, that were vegetated with sagebrush, bitterbrush, gambel's oak, and other shrubs. There was very little herbaceous understory. Mesic habitats were defined as those with moist soil, primarily facing north or east, that were predominantly vegetated with spruce-fir and having aspen and maple pockets. Percent cover afforded the bedded animal and visibility were estimated against a highly visible background of fluorescent painted sheet metal or a silver space blanket. The background was placed perpendicular to north, south, east, and west compass points from the center of the deer bed and observed from a 5 m distance perpendicular to the compass points. Percent cover was estimated as the percent of the background covered by projecting vegetation and visibility as the percent of the artificial background that could be seen through the vegetation. Data were pooled and examined using histograms for numbered beds observed compared to vegetation type and slope position and one-way analysis of variance, with $\alpha = .01$ for visibility compared to community type.

Results and Discussion

Six trends were evidenced from data analyses. There was a preference for bedding under or near conifers. Of forty-one total beds examined, including both sites, 78% ($n = 32$) were within 2 m of coniferous trees (Fig. 1). In predominantly mesic aspen communities, deer beds were primarily found in small pock-

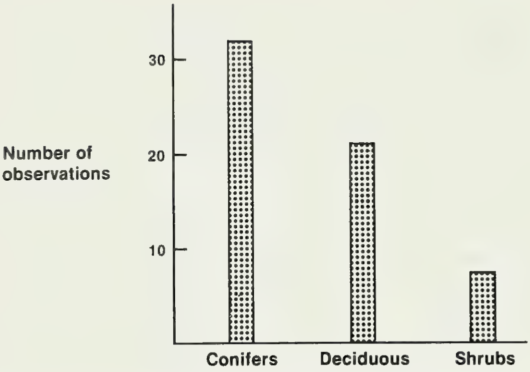

Fig. 1. Number of deer beds observed in various vegetative types. Conifers = spruce, fir, pine. Deciduous = aspen, maple, oak, chokecherry, etc. Shrubs = sagebrush, snowberry, bitterbrush, mountain mahogany, etc.

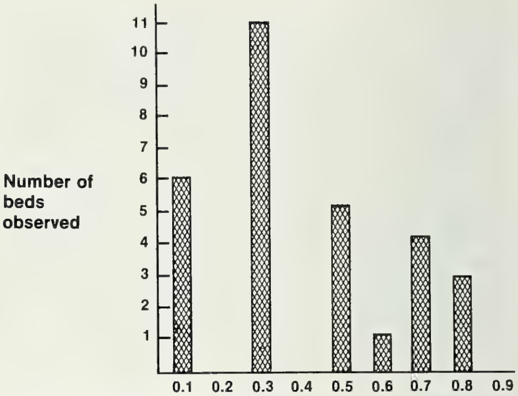

Fig. 2A. Number of deer beds found at various slope positions within mesic areas. 1.0 = top of the mountain.

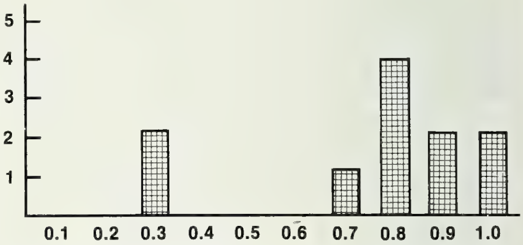

Fig. 2B. Number of deer beds found at various slope positions within xeric areas. 1.0 = top of the mountain.

ets of conifers. On the south-facing slope of Eccles Canyon, one lone fir on a xeric mountainside of predominantly oak and shrubs sheltered two well-used deer beds. Linsdale and Tomich (1953) reported that resting places suitable to some needs are likely within very limited areas that deer use repeatedly. Of special attraction is the ground beneath dense trees, where there is insulation from the weather. Moen (1973) reports that deer will remain in a bed for one to three days after a storm, usually under low-hanging conifers. He also reveals that beds of white-tailed deer in Maine were found under conifer branches that were bent down and covered with snow. In hot weather, areas under conifers are cooler than more open vegetation stands. Dark shadows also provide concealment for bedded deer. Often other types of vegetation, such as deciduous trees, forbs, or shrubs, are located proximally to the bedding community.

Aspen groves also provide choice bedding sites. They offer an abundant food supply and are often small enough to allow deer to see in all directions. Because of leaf litter and underbrush, aspen stands prohibit silent stalk or approach of predators (McRae 1980). Aspen groves were commonly used by females as evidenced by the sex of deer flushed from beds.

Eighty-seven percent (n = 36) of beds were located upon or contiguous to a deer trail. This has the advantage of allowing deer immediate access to relatively unobstructed escape routes. Energetically it is less costly to use established trails when fleeing from danger or locating a resting spot than to forge through dense brush. Trails along which deer frequently bed, therefore, are the travel lanes connecting feeding, watering, bedding, and escape areas of deer's home range (Dasmann and Taber 1956). Of the remaining beds that were not located on a trail, most were in dense cover close to trails.

Significant differences were noted in characteristics of deer beds between xeric and mesic communities with respect to elevation of beds and percentage of cover projected over the bed. Beds in xeric habitats were on the average located at higher slope positions than those in mesic communities (Fig. 2). Analysis of variance indicated that the mean percentage of projected cover over the beds in xeric areas (12.7%, n = 12) was significantly less (P = .01) than in mesic areas (38%, n = 29). This seems obvious when considering the short vegetation of xeric communities, but it may explain why xeric beds are higher altitudinally. Deer that bed in xeric habitats compensate for lack of cooling shade by selecting bedding sites at higher elevations where updrafting occurs and temperatures are cooler. Since bucks predominate in xeric communities (King and Smith 1980), the possible thermoregulatory function of antlers may help males compensate for the lack of shade in drier environments. This would be particularly true if wind currents play a role in heat dispersal. Bedding in more open higher places, without heavy concealing vegetation, provides deer with a visual advantage over predators. Many beds were located along the top of a ridge or just below the crest, where the bedded animal had commanding views of the surrounding areas.

The percentage of cover variance on the uphill side of the bed between mesic and xeric areas indicated an important trend. There was a significant difference ($P = .01$, $F = 12.37$) between cover on the uphill side of beds located in xeric areas compared to those in more mesic areas. Mean uphill cover in xeric communities was 79.1% ($n = 12$) compared to 41.0% ($n = 29$) for mesic environments. Comparisons of percent downhill cover and on both lateral sides of the beds showed no significant differences between the two habitat types. The greater amount of protective uphill cover for more open, xeric beds not only broke up the outline of the deer but provided greater visual and physical protection from predators approaching the blind side of the deer. Predators, such as cougars, are forced to go around the obstacle provided by more dense cover instead of making a direct rushing attack on the resting deer. This gives bedded deer the advantage of a head start.

Analyzing percent visibility that can be seen of the bed from the four compass points showed a common trend that holds for xeric and mesic communities. The lowest percent visibility is from the north (Table 1). This may afford greater protection from cold north winds and heat radiation to an open, air-circulating environment. There was also decreased visibility on the west side of the bed in both habitat types. This may be advantageous by affording protection to bedded deer from the hot afternoon sun.

Analysis of variance showed that the mean bed size does not vary significantly from xeric to mesic communities ($F = 0.86$, $P = .01$). This is a little surprising since Linsdale and Tomich (1953) report that deer beds conform closely to the size and shape of the body of the reclining deer and more males were found in xeric habitats. It is likely that there is no significant size difference between females and males observed.

TABLE 1. Mean percent visibility from deer beds in north, south, east, and west directions for xeric and mesic communities.

	Xeric (%)	Mesic (%)
Visibility north	9.1	38.1
Visibility south	29.6	58.6
Visibility east	28.2	56.8
Visibility west	14.1	48.6

A general observation was that no matter how steep the incline, deer beds are situated horizontally. Many beds were located in level spots created by the earth-leveling effect of tree roots. Linsdale and Tomich (1953) reported that deer bedded on steep slopes in which loose soil has been pushed downhill, creating a level site. Trails provided level resting spots on steep hillsides upon which deer frequently bedded.

Beds were selected in places where foliage was especially impenetrable and dense, providing almost complete concealment, or in high, open places where visibility was good and many escape routes were available. Does and fawns bedded more often in thickly vegetated areas. They benefit from heavy cover and rely on concealment to avoid danger. Concealment is sometimes employed by mature bucks. They often remain bedded rather than flush in response to heavy hunting pressure.

In summarizing this study, more beds were found on mesic, north-facing slopes than xeric, south-facing slopes. North-facing slopes are cooler, more densely covered, and provide a food supply with higher water content than xeric habitats. Such bedding sites provide thermoregulatory, concealment, and nutritional needs of deer, particularly females, during summer months. Many beds, used predominantly by males, were located immediately above a precipice or below cliffs, especially where steep slopes run down from the base of the cliff. This provides protection from approach on one side, excellent vision below, and convenient escape routes. Other areas where beds were consistently located included small benches or flat areas on mountainsides. These provide level places to lie on as well as excellent vantage points and backdrop cover. Included as favorite sites were shoulders or points of big ridges and patches of sagebrush or other short brush in open country. In some areas on Timpanogos, timberline is not consistent, but rather it extends in long fingers underneath cliffs. Deer often bed near the crest of the slope where these narrow strips of timber project.

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TRUMPETER SWAN (*CYGNUS BUCCINATOR*) FROM THE PLEISTOCENE OF UTAH

Alan Feduccia[1] and Charles G. Oviatt[2]

ABSTRACT.—A Trumpeter Swan (*Cygnus buccinator*) is reported from Pleistocene deposits in Utah.

Among fossil bones recovered from a deposit of Pleistocene age in Utah are numerous elements of the Trumpeter Swan (*Cygnus buccinator*)[3]. These fossils were collected by Oviatt from pre–Lake Bonneville marginal lacustrine deposits in an exposure along the West Side Canal in the NW 1/4, Sec 4, T12N, R2W, Cutler Dam, Utah, 7.5 minute quadrangle. The exposure is approximately 140 ft above the Bear River at an altitude of about 4,400 ft. The bones were excavated from a silty clay unit that contained many gastropods, including the genera *Helisoma*, *Lymnaea*, and *Valvata*.

Amino acid ratios on gastropods from this locality (W. D. McCoy, personal communication, 1984) and available radiocarbon dates indicate that the marginal lacustrine deposits are approximately 40,000 to 65,000 years old and are part of a sequence of pre–Lake Bonneville lacustrine beds well exposed in this area (Oviatt et al., 1985: 260). A soil profile at the top of the marginal lacustrine deposits is overlain by lacustrine deposits of the Bonneville Alloformation. The marginal lacustrine deposits were deposited near the shore of a lake that rose to a maximum altitude of slightly less than 4,400 feet. The presence of a lake of this size in the Bonneville basin indicates that the climate was relatively cool or moist at the time the Trumpeter Swan bones were deposited.

The elements recovered include parts of two humeri, a coracoid, radius, ulna, scapula, and pieces of vertebrae, all of which are assignable to *C. buccinator* on the basis of larger size and more robust nature when compared to similar elements of modern *Cygnus columbianus*, the Tundra Swan.

The Trumpeter Swan, the largest living swan, lives on ponds, lakes, and marshes during the breeding season, when it occurs in Alaska, and in parts of western Canada and the United States, south from Saskatchewan to southeastern Oregon, eastern Idaho, and northwestern Wyoming. It bred formerly south to Nebraska, Iowa, Missouri, and Indiana. During the winter months this swan occurs over parts of Alaska and western Canada, south to California, and occasionally to Utah, New Mexico, and Colorado (American Ornithologists' Union, 1983: 63–64). It formerly wintered south to the Mexican border, the Gulf Coast of Texas and Louisiana, and the Mississippi Valley and on the Atlantic Coast from New Jersey and Pennsylvania to North Carolina (Banko 1960: 26). It is known from Pleistocene deposits from Oregon, Illinois, and Florida and from prehistoric sites from Alaska, Iowa, Illinois, and Ohio (Brodkorb 1964: 233). Thus, this is the first Pleistocene record of the Trumpeter Swan from Utah and could well be an additional indication of the more expansive range occupied by this species in the past, because it presently only occasionally visits Utah during the winter months.

Trumpeter Swans feed primarily in shallow water, plunging the head and neck below the surface in their quest for aquatic plants growing on the bottom. This type of habitat conforms to the picture of the deposits from which these bones were recovered.

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[3] The swan bones are housed with the vertebrate paleontology collections at the Antiquities Section, Utah Division of State History, 300 Rio Grande, Salt Lake City, Utah 84101. Catalogue number UVPO99, collection locality number 42Bo049v.

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NEW SPECIES AND A NEW COMBINATION OF *MENTZELIA* SECTION *BARTONIA* (LOASACEAE) FROM THE COLORADO PLATEAU

H. Thompson[1] and B. Prigge[2]

ABSTRACT.—A new species, *Mentzelia* (sect. *Bartonia*) *cronquistii*, subfamily Mentzelioideae, is described and a new combination, *M.* (sect. *Bartonia*) *marginata* (Osterhout) is made. These two species of the Colorado Plateau are closely related to each other, but their relationships to other species in section *Bartonia* are obscure.

The plants of *Mentzelia* sect. *Bartonia* in the Colorado Plateau of eastern Utah, western Colorado, and northern Arizona show very high morphological diversity that has not been easy to analyze by standard collection and herbarium methods. The opportunity for great morphological diversity has been provided by the very high habitat diversity, the principle component of which is substrate diversity. The Colorado Plateau is composed of a variety of strata, intruded by igneous rock and tilted with a northeast dip. The Colorado River has cut through the Plateau, against the dip, exposing the various strata. A second component of this habitat diversity is elevation, for the various substrates are exposed over a gradient of over a thousand meters. A third component of diversity is rainfall, which varies geographically and with elevation. This paper factors two species from the diversity in *Mentzelia* (sect. *Bartonia*) in the Colorado Plateau, and, although recognition of these two species makes understanding the remaining diversity somewhat easier, there still exist some local endemics that need recognition, and we feel certain that additional endemics remain to be discovered.

Plants of both *Mentzelia cronquistii* and *M. marginata* have been grown in the experimental garden at UCLA, where hybridizations have been made using standard techniques of emasculation and pollen exclusion. Chromosomes have been observed with phase microscopes in squashed microsporocytes from buds fixed in 3:1 ethanol/ascetic acid. Seeds have been coated then examined and photographed with a scanning electron microscope. SEM photographs and voucher herbarium specimens for the hybridization and chromosome studies are deposited at RSA.

Mentzelia marginata **(Osterhout) Thompson & Prigge,** comb. nov.

Nuttallia marginata Osterhout. Bull. Torrey Bot. Club 49: 183. 1922.

TYPE: COLORADO, Mesa Co., DeBeque, on the hills north of town, August 22, 1918, *Osterhout* 5842 (Holotype: RM!).

Herbaceous perennial up to 25 cm tall; stems erect, single or much branched at base, white, pubescent with both glochidiate and pointed hairs; rosette leaves oblanceolate, crenate or sinuate; lower cauline leaves oblanceolate to broadly ovate, 3–6 cm long, 1–2 cm wide, with the lowermost petiolate, with upper ones smaller, oval, sessile, broad and somewhat clasping; lower leaf surfaces densely pubescent with long and short glochidiate hairs and scattered pointed hairs; upper leaf surfaces more sparsely pubescent with pointed hairs; leaf margins with large glochidiate hairs; bract at base of capsules linear and entire; flowering period June through August; flowers opening in late afternoon; calyx lobes 5–8 mm long; petals 5, yellow, 10–13 mm long, 2–5 mm wide, pubescent on outer surface, ovate to narrowly ovate, acute at apex; the next whorl within the petals 5 petaloid stamens, pubescent at base, similar in shape to the petals but smaller, only 3 mm wide and with functional anthers; stamens numerous, grading in length from 3 mm for the innermost to 10 mm for the outermost, with narrow filaments for innermost ones and

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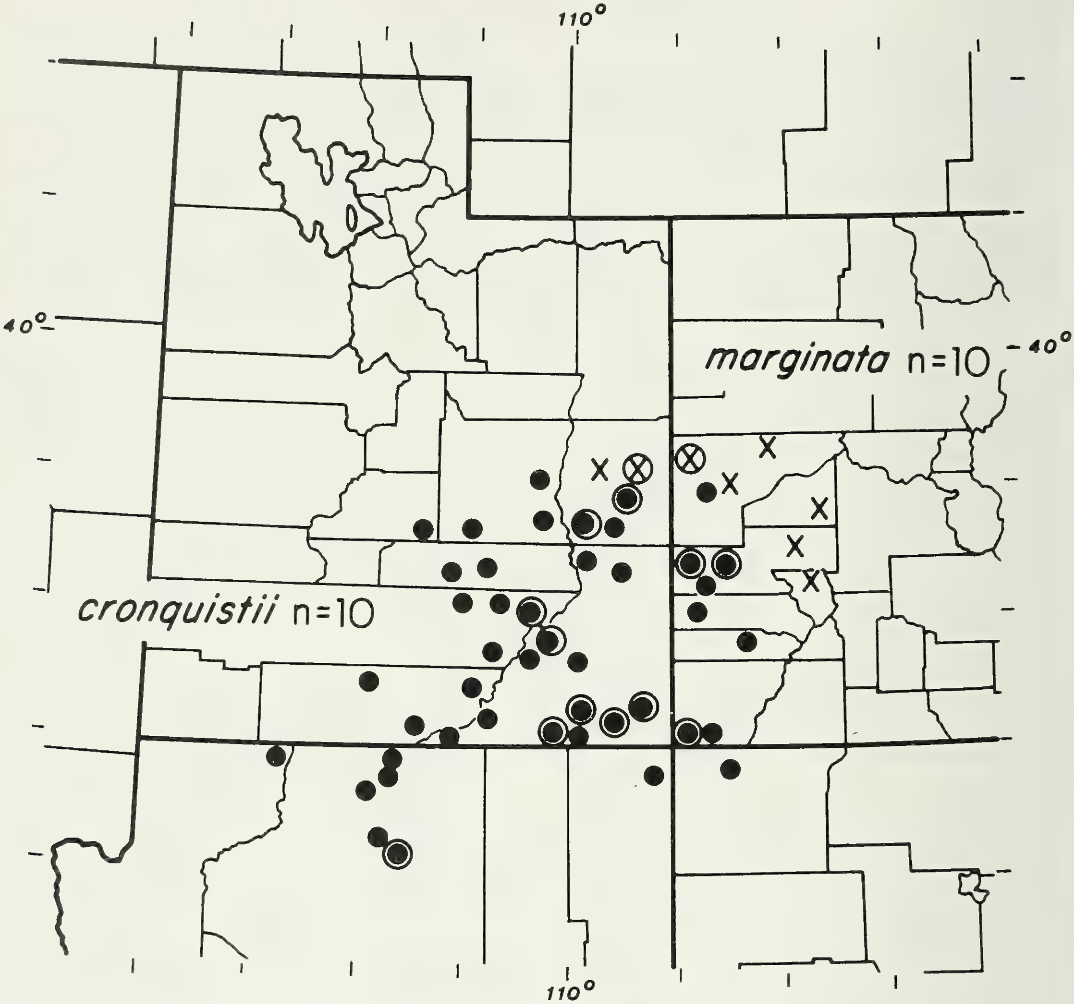

Fig. 1. Distribution map of *Mentzelia cronquistii* and *M. marginata*.

broader filaments for outermost ones; styles 6–10 mm long; capsules cup shaped to subcylindrical, 8–12 mm long; seeds lenticular, oblong to somewhat ovate, 2.5–2.7 mm long, 1.7–1.8 mm wide, including the narrow wing, which is 0.2 mm wide; seed surface tan to dark grey, tessellate, strongly colliculate; seed coat cells with the radial walls straight, with center of outer tangential walls raised with 10–20 papillae; chromosome number $n = 10$; self-incompatible.

Specimens examined: UTAH. Grand Co.: 2 mi E of Thompson, *Ripley & Barneby 8659* (CAS, NY); 1 mi W of Cisco, *Ripley & Barneby 9209* (CAS); Cisco, *Thompson 3518* (LA, chromosome voucher $n = 10$), *Thompson 3532* (LA). COLORADO. Mesa Co.: 15 mi W of Fruita, *Rollins 1936* (GH); 12.8 mi W of Fruita, *Thompson 3519* (LA, chromosome voucher $n = 10$); 5 mi W of Mack, *Brown* in 1938 (CS); De Beque, *Osterhout 4284* (NY), *Osterhout 4724* (GH); near Whitewater, *Simonds* in 1948 (CS). Delta Co.: 5 mi NW of Eckert, *Weber 7527* (COLO, WS); Paonia, *Osterhout 4601* (NY, RM). Montrose Co.: Montrose, *Shear 4810* (NY, US). Ouray Co.: near Colona, *Payson 2334* (RM).

Mentzelia marginata occurs in eastern Utah and western Colorado (Fig. 1) in open habitats in juniper woodland at elevations between 1,400 and 1,800 m. Populations are restricted to grey clay soils often associated with coal.

***Mentzelia cronquistii* Thompson & Prigge**, sp. nov. (Fig. 2)

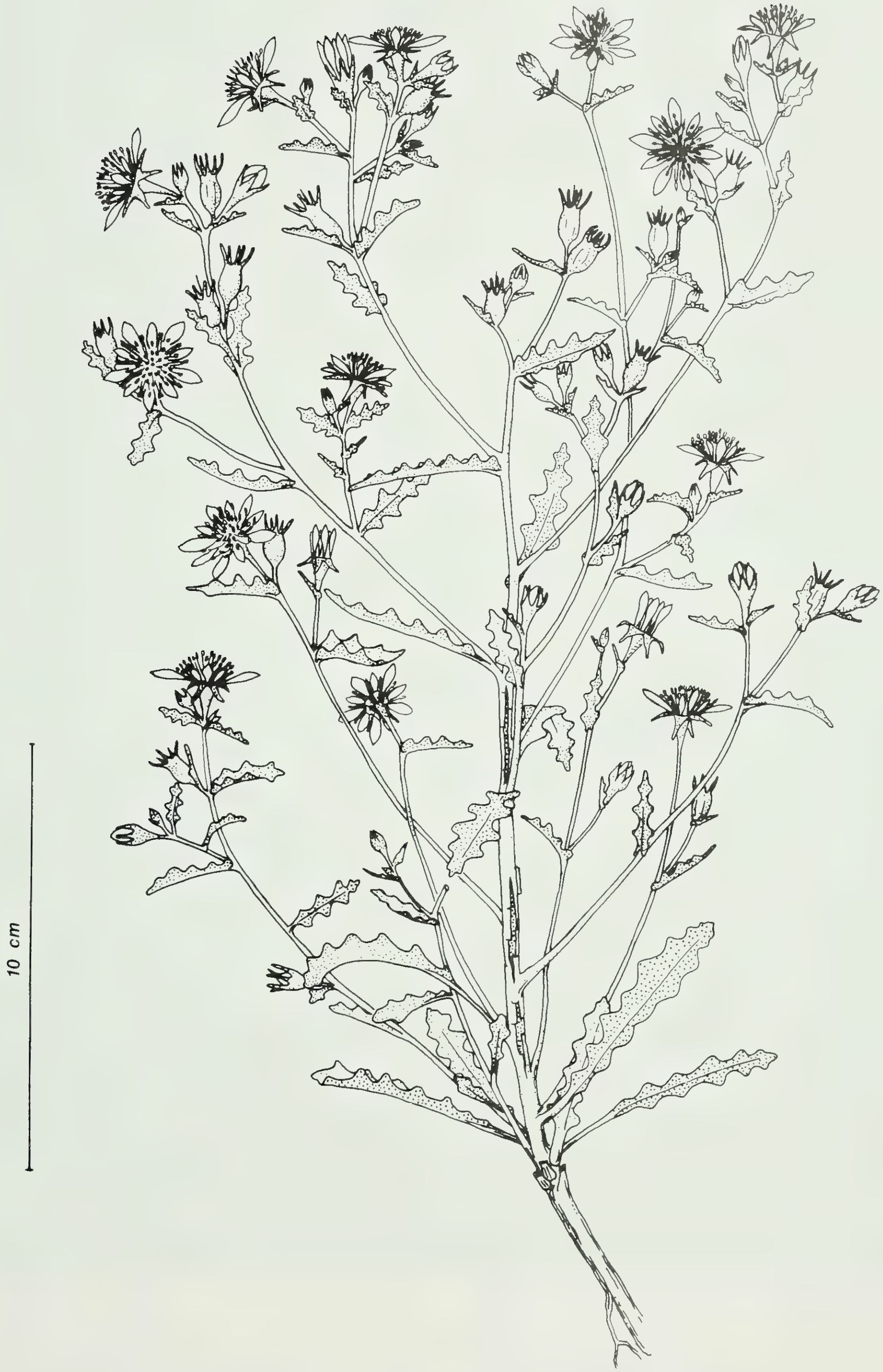

Fig. 2. *Mentzelia cronquistii,* drawn from *Prigge 6643* (LA).

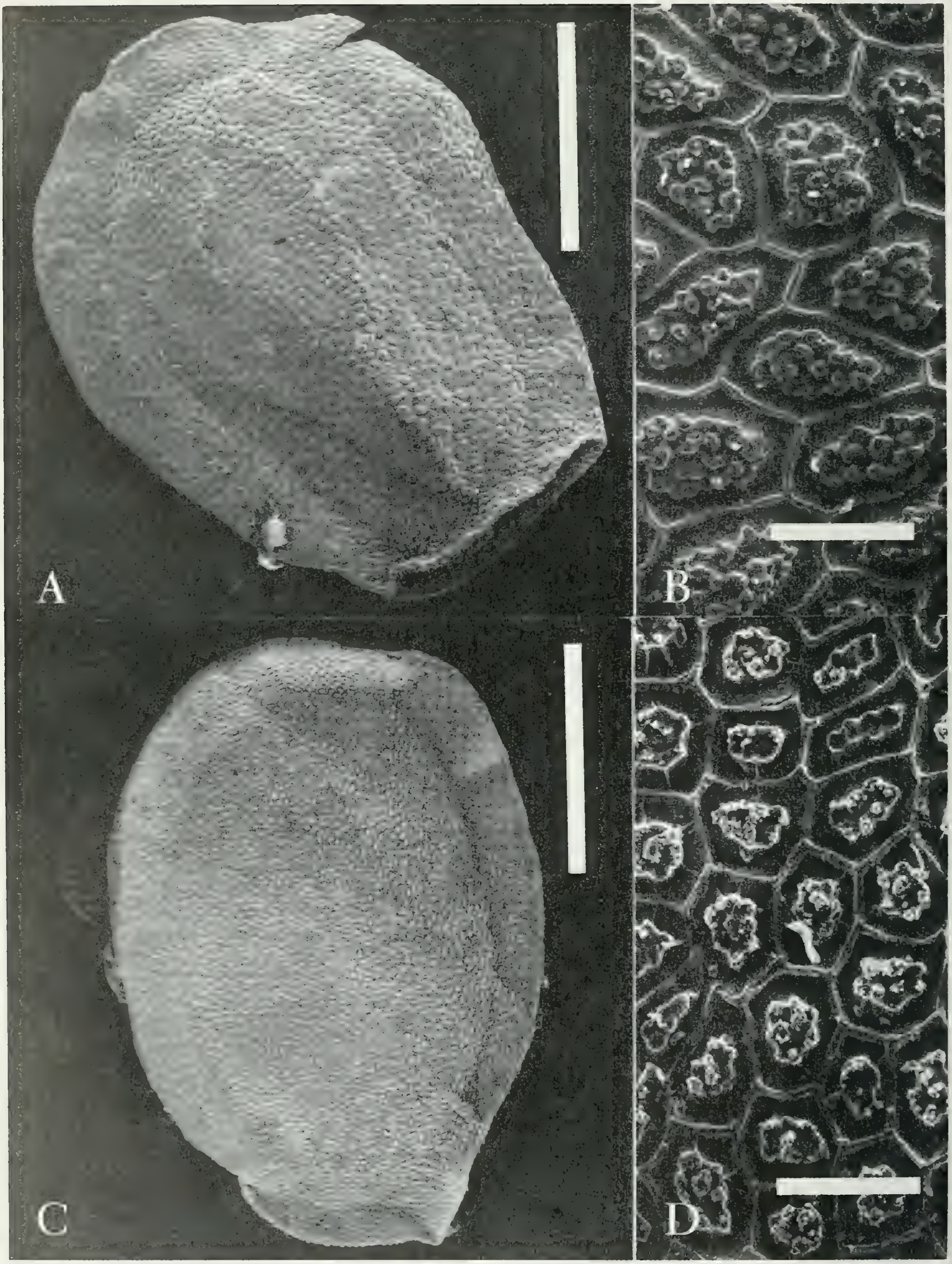

Fig. 3. Scanning electron micrographs of seeds of *Mentzelia cronquistii* (A and B) and *M. marginata* (C and D). A and C are of whole seed (bar = 1 mm). B and D are of seed coat (bar = 0.05 mm).

Similis *M. marginata* sed in lobis rhachidis angustioribus et lobis brevis, floribus cum 10 petalis et staminibus petaloideis nullis, et testa cellulis majoribus, parietibus radialium

undulatus leviter vel bono modo, et plus papillatis differt.

Herbaceous perennial 15–40 (−50) cm tall; stems erect, single or much branched at base, reddish colored under the surface layer, pubescent with both glochidiate and pointed hairs; rosette leaves lanceolate to oblanceolate, shallowly and bluntly lobed; lower cauline leaves lanceolate, 2.5–8 cm long, lobed, with the rachis 2–5 mm wide and the lobes 2–10 mm long, thus the leaves 5–15 mm wide; upper leaves shorter and narrower, with the lobes shorter and more pointed; lower leaf surfaces densely pubescent with long and short glochidiate hairs and scattered pointed hairs; upper leaf surfaces more sparsely pubescent with pointed hairs and small glochidiate hairs; leaf margins with large glochidiate hairs; bracts at base of capsules linear and entire; flowering period late May to September; flowers opening in late afternoon; calyx lobes 6–9 mm long; petals 10, yellow, 7–13 (−15) mm long, 2–5 mm wide, pubescent on outer surface, narrowly ovate to narrowly obovate, rounded to acute at apex, with inner 5 shorter and narrower than outer 5; stamens numerous, grading in length from 5 mm for the innermost to 9 mm for the outermost; with narrow filaments for inner ones and wide filaments, to 2.5 mm wide, for the outer ones; styles 6–10 mm long; capsules cup shaped, 6–13 mm long; seeds lenticular, oblong to ovate, 2.4–2.7 mm long, 1.8–2.0 mm wide, including the narrow wing, which is 0.25 mm wide; seed surface tan to dark grey, tessellate, strongly colliculate; seed coat cells with the radial walls slightly to moderately wavy and center of outer tangential walls raised with 15–25 papillae; chromosome number $n = 10$; self-incompatible.

TYPE: UTAH, San Juan Co., about 75 mi W of Blanding and 10 mi E of Hite, May 16, 1961, *Cronquist 9030* (Holotype NY!; isotypes LA!, WS!, WTC!, UTC!). Seed from *Cronquist 9030* has been grown in the greenhouse at UCLA, mature plants showed a chromosome number of $n = 10$, voucher *Thompson 3296* (LA).

ADDITIONAL SPECIMENS EXAMINED: More than 100 specimens were examined from the following herbaria: ARIZ, ASU, BRY, CAS, COLO, CS, GH, LA, MO, MICH, NY, POM, RM, RSA, SMU, UC, US, UT, WTU, and WS. A list of these specimens is available on request from LA.

Mentzelia cronquistii occurs in southeastern Utah, southwestern Colorado, northwestern New Mexico, and northeastern Arizona (Fig. 1) in open, often disturbed habitats in juniper woodland at elevations between 1,100 and 1,800 m. Populations are most well developed on fine- to medium-grained sand from red sandstone, but populations also occur on rocky talus and in sandy washes. Roadsides are good sites for *Mentzelia cronquistii*, and the range and abundance of the species may have increased with the development of roads.

The specific epithet honors Dr. Arthur C. Cronquist, student of angiosperm phylogeny, systematics of the Asteraceae, and floristics of the western United States.

Mentzelia cronquistii and *M. marginata* are more similar to each other than to any other species. They both possess petals that are pubescent on their outer surfaces, a characteristic possessed by no other species of *Mentzelia*. All species of *Mentzelia*, and probably all species of Loasaceae, have petals with a few hairs at the apex of the petals, but pubescent petals such as occur in *M. cronquistii* and *M. marginata* occur only in those two species and in some South American species of *Loasa* and *Caiophora* of subfamily Loasoideae. The seeds of *M. cronquistii* and *M. marginata* are also very similar, differing only in that the seed coat radial walls of *M. cronquistii* are more wavy than those in *M. marginata* and the seed coat cells in *M. marginata* are somewhat smaller (Fig. 3), making the seeds of *M. marginata* appear smoother when viewed with 10X magnification.

Mentzelia cronquistii differs in two conspicuous characters—petal number and leaf shape. *Mentzelia cronquistii* has 10 petals, whereas *M. marginata* has only 5. In *M. cronquistii* the whorl immediately within the petals is composed of stamens with narrow filaments, but in *M. marginata* the whorls within the petals are petaloid stamens, stamens with broad filaments, and then stamens with narrow filaments (Fig. 4). The second conspicuous difference between *M. cronquistii* and *M. marginata* is in leaf shape. The leaves of *M. cronquistii* have a narrow rachis with short or long lobes, whereas the leaves of *M. marginata* are broad with crenate margins.

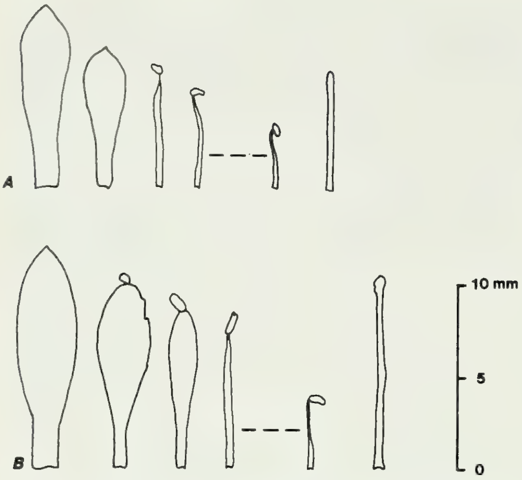

Fig. 4. Elements of the floral whorls. A. *Mentzelia cronquistii* from left to right: outer whorl petal, inner whorl petal, outermost stamen, stamen - - - innermost stamen, style. B. *M. marginata* from left to right: petal, petaloid stamen, outermost stamen, stamen stamen - - - innermost stamen, style.

We have grown individuals of *M. cronquistii* and *M. marginata* in the experimental garden at UCLA. Voucher specimens of parent plants, siblings, and F_1 hybrids are deposited at RSA. The data for these crosses are given with the specimens and should be consulted by anyone interested in these species. In summary, these data show that both *M. cronquistii* and *M. marginata* are self-incompatible. Sibling plants are vigorous and fertile. The hybrids of *marginata* ♀ × cronquistii ♂ and reciprocals are vigorous but sterile, producing less than 10% good pollen and forming no viable seed in both backcrosses and sibling crosses.

ACKNOWLEDGMENTS

We thank Dr. Stanley L. Welsh for providing the latin diagnosis.

NEW VARIETY OF *MENTZELIA MULTICAULIS* (LOASACEAE) FROM THE BOOK CLIFFS OF UTAH

Kaye H. Thorne[1] and Frank J. Smith[2]

ABSTRACT.—Described is *Mentzelia multicaulis* (Osterh.) Goodman var. *librina* Thorne & F. J. Smith.

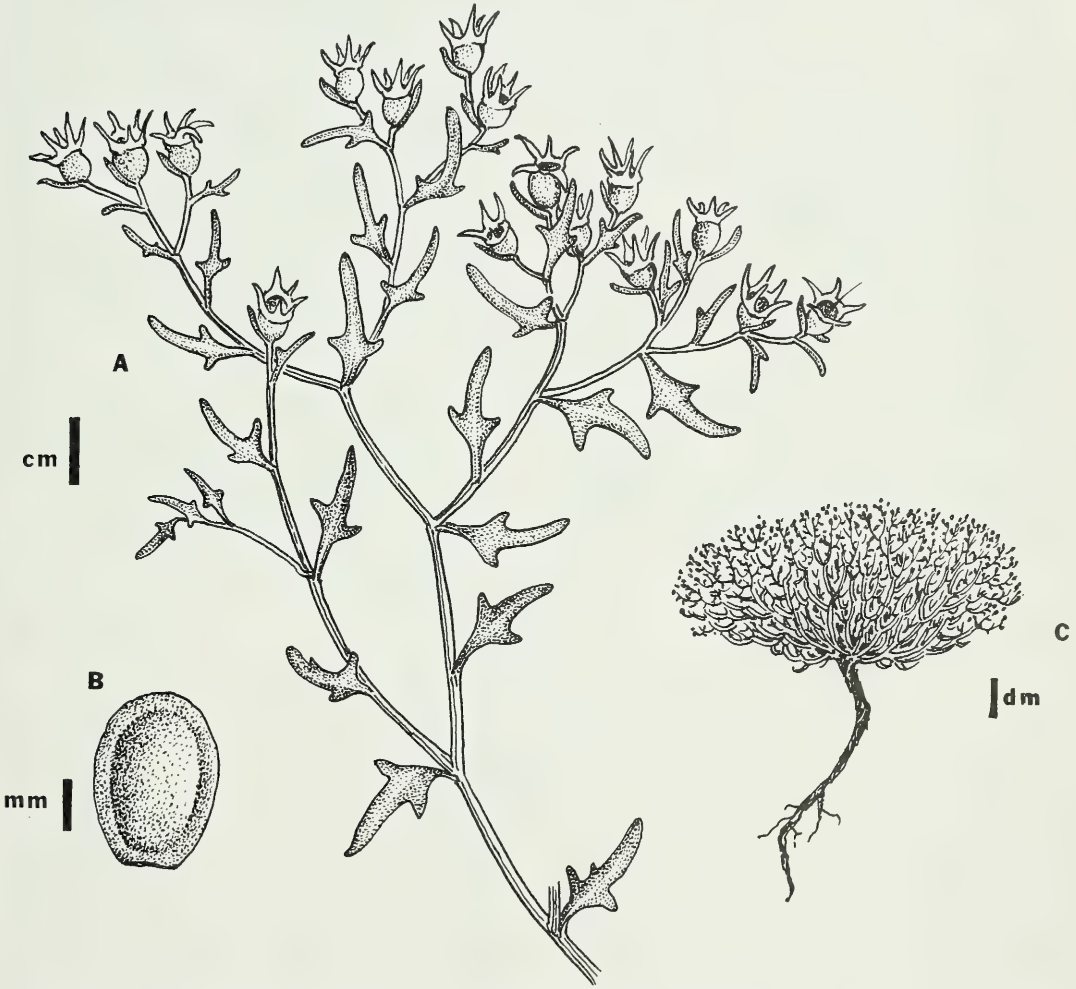

Fig. 1 *Mentzelia multicaulis* (Osterh.) Goodman var. *librina* Thorne & F. J. Smith: A, Branch. B, Seed. C, Habit.

Mentzelia multicaulis (Osterh.) Goodman is a suffrutescent perennial endemic to Uintah, southeastern Duchesne, eastern Carbon, and northeastern Emery counties in Utah and western Rio Blanco County, Colorado. The plant is characterized by a diffusely branched

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Recent work by Dr. H. J. Thompson (personal communication) has suggested the presence of a previously undescribed *Mentzelia* in Utah and eastern Nevada that has been variously treated as *M. pumila* (Nutt.) T. & G. or as *M. laciniata* (Rydb.) Darlington. The plants show morphological similarity to the former in capsule shape and flower size, and to the latter in the deeply pinnatifid leaves with narrowly acute lobes. The undescribed material appears to be more nearly allied to *M. pumila* than to *M. laciniata*, sharing the same base chromosome number (x = 11, fide H. J. Thompson 3513, Atsatt 646 and 649, Garfield Co., H. J. Thompson 3516, Wayne Co., LA) and habit of growth. The plants differ from *M. pumila* var. *pumila* in having basal leaves deeply pinnatifid, with lobes acute to obtuse, upper leaves narrowly lanceolate and pinnatifid almost to the midvein, bracts remotely pinnatifid with 1 or 2 lobes or entire, seeds winged, gray 3–3.5 mm long, and cell walls of the seed coat undulate. The material is therefore described as follows.

Mentzelia pumila **(Nutt.) T. & G. var.** ***lagarosa*** **Thorne** var. nov. Similis var. *pumila* generalis sed in foliis basalium pinnatifidis profunde et lobis acutis vel obtusis foliis caulinorum lanceolatis anguste fissis propre venis bracteis pinnatifidis remotis 1-vel 2-lobatis seminibus 3–3.5 mm longis (nec minus 3) et cellula parietis undulatis.

TYPE: USA: **Utah**. Uintah Co., T11S, R24E, S11, near Watson, Evacuation Creek, 10 miles 173 degrees from Bonanza, 1,708 m, on gravel, 1 August 1980, S. Goodrich & N. D. Atwood 14664 (Holotype BRY; 3 isotypes distributed previously as *Mentzelia*).

ADDITIONAL SPECIMENS: **Utah**. Duchesne Co., T5S, R3W, S5, West Tavaputs Plateau, in Antelope Canyon, 24 km 67 degrees from Duchesne, 1,769 m, calcareous hills, Uinta Formation, 25 August 1980, S. Goodrich 14972. Kane Co., 14 miles SE of Cannonville along Cottonwood Wash road, pass between Round Valley Draw and Butler Valley, on roadside cut, 1,830 m, 21 June 1983, B. Albee 5564. Piute Co., T30S, R1W, S32, Dry Fork Canyon, ca 2 km NE of Antimony, 2,288 m, in pinyon-juniper community, on sandy gravel, 28 July 1976, S. L. Welsh, K. Taylor, & G. Moore 14120. **Nevada**. Lincoln Co., T3N, R70E, S16, ca 2 km on road to Hamlin Valley, Eagle Valley, White Rocks Range, at 1,830 m, grassland—mixed desert shrub community on rocky limestone and clay exposed slopes, 22 August 1979, K. H. Thorne and J. Thorne 775 (all BRY).

AGATHOXYLON LEMONII SP. NOV., FROM THE DAKOTA FORMATION, UTAH

William D. Tidwell[1] and Gregory F. Thayn[2]

ABSTRACT.—Petrified wood specimens from the Dakota Formation of Utah are here described as *Agathoxylon lemonii*. This new species is characterized by having distinct growth rings, araucarian tracheary pitting, resin plates or plugs in its tracheids, abundant axial parenchyma, low uniseriate rays and 1–4 small, slightly bordered pits with circular to oval included apertures per crossfield. This is the first report of petrified wood from the Dakota Formation of the western United States and the first record of *Agathoxylon* from North America.

Although fossil plant remains are abundant in the Dakota Formation, reports of petrified plant material from this formation are rare. The study of fossil plants in the Dakota Formation began in the midwestern United States. Initial collections of fossil plants from this formation were obtained during western territorial surveys for a proposed route for a transcontinental railroad in the 1850s and 1860s (Dilcher et al. 1978). Hayden, in 1853, was the first to obtain leaves from the Dakota Group of Nebraska. He and Meek in 1856–57 collected additional plant materials from these sediments that were subsequently sent to Professor Oswald Heer in Switzerland for study. Heer (1859) published descriptions of these materials. This publication represents the first authentic record of North American Cretaceous plant fossils.

Well-preserved leaves were later collected in large numbers in Kansas during the 1860s and 1880s by various workers. These collections formed the basis for the first major publications on this flora by Lesquereux (1874, 1883, 1892).

Subsequent to Lesquereux's publications, very little work had been done on the flora of the Dakota Formation until recently, when considerable research on the reproductive structures and leaves of early angiosperms from this formation in Kansas was published (Dilcher et al. 1976, Dilcher et al. 1978, Dilcher 1979, Retallack and Dilcher 1981).

The Dakota Formation extends throughout much of the southwestern and midwestern United States. Stanton (1905) in working with Jurassic and Cretaceous formations and the Dakota in southern Colorado, New Mexico, and Oklahoma, demonstrated that the Dakota Formation of this region, as originally defined, contains both Lower and Upper Cretaceous strata. In Utah the Dakota Formation occurs between the Lower Cretaceous Cedar Mountain Formation and the Upper Cretaceous Mancos Shale and is considered to be mid-Cretaceous in age. Fossil plants in the Dakota Formation of western Colorado and eastern Utah were first reported by Brown (1950) and later by Tidwell et al. (1967), Rushforth and Tidwell (1968), and Rushforth (1970, 1971).

Brown (1950) described a flora from the Burro Canyon Formation that is more or less equivalent to at least a portion of the Cedar Mountain Formation (Young 1960, Tschudy et al. 1984) and a flora from the Dakota Formation near Naturita, Colorado. This flora, like the Dakota flora from Westwater, Utah, is atypical in that the percentage of ferns is high as compared with the number of angiosperms. The Dakota flora near Westwater is dominated by the ferns *Astralopteris* Tidwell, Rushforth, and Reveal, *Matonidium* Schenk, *Gleichenia* Smith, *Hausmania* Dunker, *Asplenium* L., *Cladophlebis* Brong., and *Coniopteris* Brong. (Rushforth 1970, 1971). No coniferous foliage has been reported from this flora in Utah. However, Retallack and Dilcher (1981) noted that *Sequoia*-like foliage, cones, and cone scales were common conifer megafossil material in the Dakota Formation

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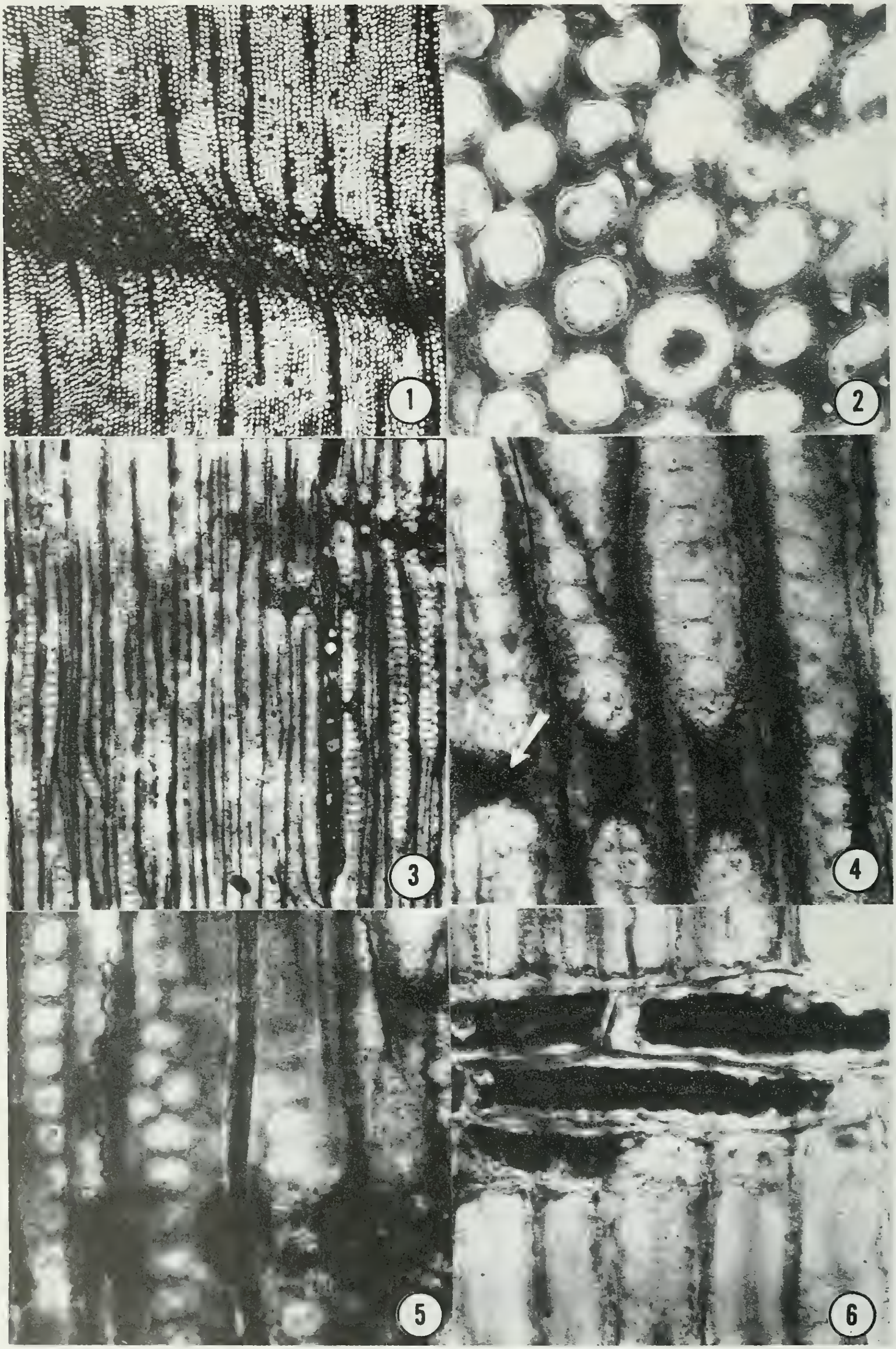
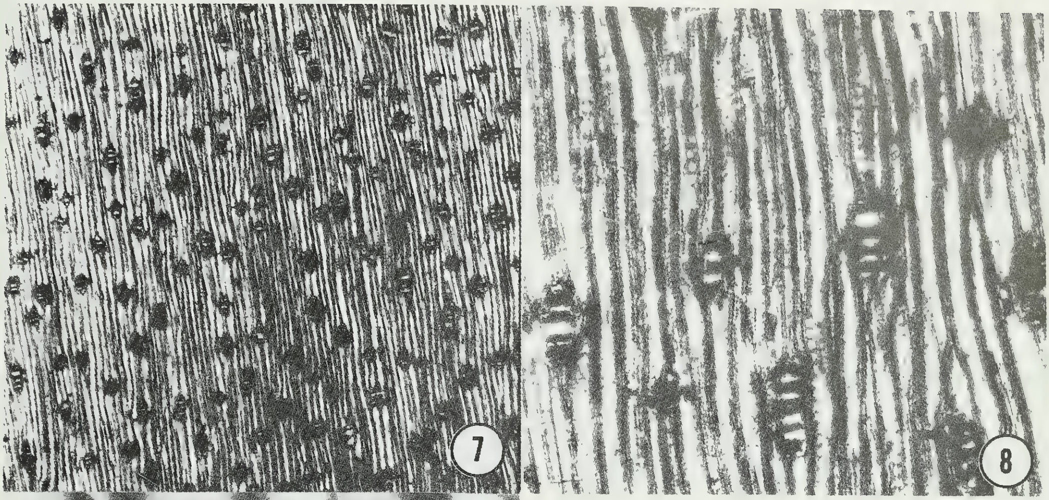


Figs. 1–6. *Agathoxylon lemonii*: 1, Transverse section illustrating a growth ring and dark axial parenchyma. (33X) (Holotype). 2, Transverse section illustrating an axial parenchyma cell with dark contents and overlapping tracheids (495 X) (Holotype). 3, Radial section illustrating axial parenchyma, radial intertracheary pitting and resin plates (123X) (Holotype). 4, Radial section illustrating uniseriate and biseriate pitting. Note resin plates in lower portion of photograph (495X) (Holotype). 5, Radial section showing a close up of radial pits. Note both elliptic and circular apertures (495X) (Holotype). 6, Radial section illustrating the nature of the ray cell walls and contents. Note crossfield pitting in the right portion of the photograph and showing through dark cell contents in upper right side ray cell (495X) (Holotype).



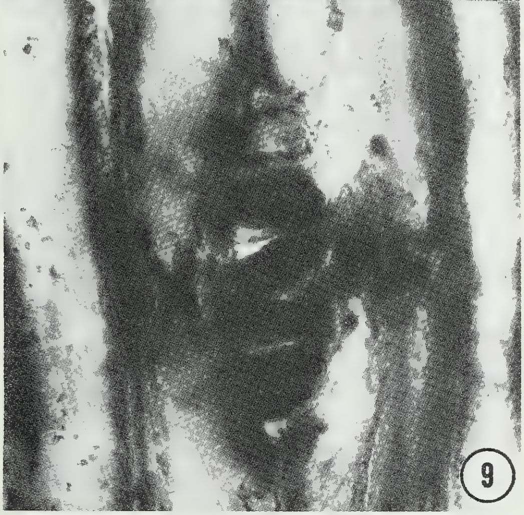


Fig. 7–9. *Agathoxylon lemonii*: 7, Tangential section showing general size, shape, and arrangement of the rays (33X) (Holotype). 8, Tangential section illustrating ray size and shape. Note tangential tracheid pitting. (123X) (Holotype). 9, Tangential section showing outline of ray and ray cells (495X) (Holotype).

in Kansas. They also noted the presence of *Brachyphyllum*, which, although not common, was evidently a minor constituent of the fossil angiospermous swamp woodland flora of this formation. Possible conifer dominance in the inland vegetation of the Dakota flora is supported by a number of palynological studies of this formation and rock units of equivalent age in North America (Pierce 1961, Agasie 1969, Romans 1975, Retallack and Dilcher 1981).

SYSTEMATICS

Coniferales

Agathoxylon Hartig

Agathoxylon lemonii sp. nov.

Figs. 1–9

DIAGNOSIS.—Growth rings distinct, 2–6 mm wide; transition from early to late wood gradual; tracheids generally hexagonal in transverse section, some compressed and oval in outline, approximately 50 μm in diameter, some slightly elongated radially, walls approximately 10 μm thick, tips of adjacent tracheids appearing in cross section as intercellular spaces often lending an appearance of collenchyma to the xylem; radial pitting generally uniseriate, frequently biseriate, pits slightly appressed, circular to horizontally elongate, 12–14 μm diameter with 2.4–7.8 μm apertures; tangential pitting uniseriate with pits same size as radial pitting, generally isolated; resin plates or plugs observed in many tracheids; axial parenchyma abundant, diffuse, with smooth thick walls and dark intercellular contents; rays uniseriate, homocellular, approximately six per millimeter, 20–70 μm wide, 10 (commonly 5 or 6) cells high, 30–150 μm high; ray cells vertically flattened and elongate horizontally, nearly twice as wide tangentially as high, often 50 μm wide tangentially by 30 μm in vertical dimension and 30–100 μm (average 70 μm) in radial dimension; ray cells filled with dark cell contents, ray cell walls approximately 3 μm thick and unpitted except at crossfield; crossfield pits commonly obscured by cell contents, observable crossfields with 1–4, small (approximately 5 μm), slightly bordered pits with circular to oval included apertures.

REPOSITORY: Brigham Young University, 5029 (Holotype).

LOCALITIES: 7 mi (11.2 km) east of Ferron, Utah; U.S. Geol. Surv. Map: Desert Lake Quadrangle, SE 1/4, Sec 26, T20S, R8E (Holotype). Other specimen: 2.5 mi (4.02 km) north of Westwater, Utah.

HORIZON: Dakota Formation.

AGE: Lower Upper Cretaceous (Cenomanian).

ETYMOLOGY: The specific epithet is for Mr. and Mrs. Frank Lemon of Moab, Utah, who donated specimens for this study.

DISCUSSION

The presence of araucarian tracheary pitting and of resin cysts, plugs, plates or spools in *Agathoxylon lemonii* indicate that it is allied to the Araucariaceae. The Araucariaceae consist of two extant genera, *Araucaria* De Jussieu with 18 species (De Laubenfels 1972) and *Agathis* Salisbury composed of 13 species (Whitmore 1980). Fossil woods with araucarian structure are abundant in the geologic record. They range in age from Carboniferous to Recent and have been assigned to many genera, including *Araucarites* Presl, *Pinites* Lindl. & Hutton sensu Presl, *Dadoxylon* Endlicher, *Araucarioxylon* Kraus, *Agathoxylon* Hartig, and *Araucariopitys* Jeffrey. These woods may also be related to *Cordaioxylon* Gr. Eury, *Cordaites* Unger, or early conifers such as *Lebachia* Florin or *Ernestodendron* Florin. Knowlton (1899), Penhallow (1907), Stopes (1914), Holden (1914), and Jeffrey (1926) assigned Paleozoic araucarian woods to *Dadoxylon* and reserved the name *Araucarioxylon* for Mesozoic and Tertiary materials. Further, Seward (1919) proposed adding qualifying terms such as *Araucarioxylon* or *Cordaioxylon* in parenthesis after *Dadoxylon* whenever evidence supports such designation. Torrey (1923) agreed somewhat with using *Araucarioxylon* for Mesozoic and Cenozoic woods and *Dadoxylon* for Late Paleozoic types. However, he also separated them by assigning *Dadoxylon* to fossil woods lacking wood (axillary) parenchyma and assigning woods with parenchyma to *Araucarioxylon*. Edwards (1921) proposed using *Dadoxylon* for araucariaceous wood that could not be related to either *Agathis* or *Araucaria*. Some authors, such as Krausel and Jain (1963), Sah and Jain (1963), and Vogellehner (1964) followed Gothan's (1905) recommendation that all woods having an anatomical similarity to Araucarineae or Cordaiteae should be placed into *Dadoxylon* as a single nomenclatural unit. Krausel (1949) designated *Araucarioxylon* as the genus for all woods related to *Agathis* or *Araucaria*. Hartig (1848) instituted the genus *Agathoxylon* for fossil having "zellfasern" or axial parenchyma woods similar to the living genus *Agathis*. The presence of axial or wood parenchyma is the only character absent or rarely found in *Araucaria*. Krausel and Jain (1963), in discussing *Agathoxylon* remarked that Hartig had not given any details of his specimen. Sah and Jain (1963) went further and suggested that the "zellfasern" of the Hartig specimen were perhaps resinous tracheids. According to Seward (1919), resin plates in tracheids are often interpreted as end walls of axial parenchyma, thus leading to erroneous reports of *Agathoxylon*. Greguss (1955), Jane (1970), and Stockey (1982) considered the anatomical separation between *Agathis* and *Araucaria* on the basis of wood anatomy to be not only difficult but nearly impossible. Greguss (1967) later reversed himself by pointing out that, of the living species in the Araucariaceae, only those in the genus *Agathis* contain true axial parenchyma, and subsequently he assigned two species to *Agathoxylon*. The fact that the Dakota wood under study bears axial parenchyma places it in *Agathoxylon*.

Members of the genus *Araucariopitys* bear short shoots, have resin ducts and abietinous crossfield pitting, and are, therefore, not related to this wood from the Dakota Formation.

COMPARISON

Of the living species of *Agathis*, *Agathoxylon lemonii* bears striking resemblance to the wood of *Agathis hypoleuca*. It differs from *A. hypoleuca* in having higher rays (1–10 cells high as opposed to 1–4 cells in *A. hypoleuca*), fewer pits per crossfield (1–4 in *A. lemonii*, 4–8 in *A. hypoleuca*), and more abundant axial parenchyma.

Dadoxylon septentrionale Gothan (1905) differs from *A. lemonii* in having typically 2–4 elliptical to oblique crossfield pits and lacking tangential pitting. *Dadoxylon eocenum* Chitaley (1949) and *Dadoxylon* (*Araucarioxylon*) *japonicum* Shimakura (1936) have tangential pitting, but both lack the xylem parenchyma of *A. lemonii*. *Dadoxylon agathoides* Krausel & Jain from the Jurassic of India is similar to the Dakota specimen. However, it lacks axial parenchyma, has higher, narrower rays and has crossfield pits that are arranged in clusters.

Araucarioxylon texense Torrey has axial parenchyma and pitting similar to the specimen from the Dakota Formation, although *A. texense* has narrower rays and short shoots, which *A. lemonii* lacks. *Araucarioxylon hoppertonae* Knowlton from the Cretaceous of the Black Hills is similar to *A. lemonii* in having few pits per crossfield and low rays, but it lacks the characteristic axial parenchyma. Holden (1914) mentioned an araucarian type wood from the Cretaceous of New Jersey (Raritan Formation) whose pith contains large masses of stone cells similar to those in living *Agathis* but lacks wood parenchyma. *Dadoxylon noveboracense* (Holl. & Jeff.) from the mid-Cretaceous beds of Staten Island lacks definite growth rings and has uniseriate tracheary pitting. These characters are similar to *A. wyomingense* Andrews and Pannell (1942) from Cretaceous strata of Gros Ventre Canyon in Wyoming. *Araucarioxylon wyomingense* lacks the wood parenchyma and tangential pitting that separates this species from *A. lemonii*.

Among the species belonging to this genus described from the Mesozoic of Africa, the following four possess wood parenchyma (Gazeau 1969): *D.* (*A.*) *aegyptiacum* Unger (1859), *D.* (*A.*) *paumieri* Loubiere (1935), *D.* (*A.*) *septatum* Boureau (1951) from the Sahara Soudanais, and *D.* (*A.*) *koufraense* Batton (1965) from the continental series of Libya. They differ from *A. lemonii*, in general, by having different ray height, different tracheary pitting, and, with some, having septations in their tracheids.

Dadoxylon alpinum Lemoigne (1966) from the Jurassic of the Bassin de la Durance has wood parenchyma, but it differs from *A. lemonii* in possessing septate tracheids, having large crossfield pits with large lumens, and lacking tangential pitting. *Dadoxylon (Araucarioxylon) breveradiatum* (Lignier) Seward from the Cenomanian of Normandy has abundant resiniferous parenchyma, but it differs from *A. lemonii* by having higher rays (4–80, usually 10–40, cells high) and septate tracheids.

Dadoxylon (Araucarioxylon) novaezeelandii (Stopes) Seward from the Cretaceous of New Zealand has well-marked growth rings, resin plates, and araucarian pitting. However, it differs from the Dakota Formation species in its lack of wood parenchyma and having thick-walled tracheids on each side of the rays.

There are a few reported species of *Dadoxylon* or *Araucarioxylon* from Japan that are similar to *Agathoxylon lemonii*. *Dadoxylon (Araucarioxylon) sidugawaense* Shimakura (1936) from the Jurassic of Miyagi Prefecture is similar in possessing distinct growth rings, similar radial pitting, tangential pitting, and, in the presence of xylem, parenchyma. But *D. (A). sidugawaense* differs from the former species in having circular, alternate tangential pits and simple crossfield pits, whereas the tangential pits of *A. lemonii* are the same size as the pits on the radial walls. These tangential pits are isolated rather than contiguous, and the crossfield pits of the latter species are slightly bordered rather than simple. Two Lower Cretaceous species from Japan, *Araucarioxylon hujinamiense* Ogura (1960) from Wakayama and Chiba and *A. pseudo-hujinamiense* Nishida and Oishi (1982) from the Kwanto Mountain, both differ from *A. lemonii* in possessing tylosislike structures in their tracheids and in lacking wood parenchyma. *Araucarioxylon nihongii* Nishida and Nishida (1984) is quite similar to this Dakota Formation species. The Japanese species, however, has 3–5 rows of pits on its tracheid walls, has shorter parenchyma cells, and lacks tangential pitting.

Agathoxylon species similar to *Agathoxylon lemonii* include *A. australe* Evans, *A. hungaricum* (Andreanszky) Greguss, and *A. mecsekense* Greguss. *Agathoxylon australe* is a Pliocene fossil from New Zealand that has vestured pits and lacks axial parenchyma.

Evans (1934) originally assigned this species to *Agathis* and later renamed it *Agathoxylon australe* (Evans 1937). Krausel and Jain (1963) noted that *Agathoxylon australe* is very similar to living *Agathis australis*. *Agathoxylon mecsekense* from the Jurassic of Hungary has high, narrow rays and commonly has triseriate pitting. Although the description given for *A. hungaricum* is incomplete, it appears to have higher rays and more pits per crossfield than our specimen.

PALEOECOLOGY

The extant genus *Agathis* may be found growing in association with the fern *Matonia* in the tropical uplands of the Malay Peninsula and the island of Borneo (Seward 1899). Morphologically, the fossil genus *Matonidium* is similar to the extant *Matonia* (Berry 1919). *Matonidium* occurs in abundance in the Dakota Formation near Westwater, Utah, a locality quite close to a collecting site for *Agathoxylon lemonii*. Mahabale (1954) considered matoniaceous ferns to be among a select group of ferns that served as reliable indicators of subtropical to tropical paleoclimate; the presence of abundant *Matonidium* is, therefore, suggestive of a similarly warm, climatic regime during the deposition of this formation in this area. This reconstruction is supported by Roman's (1972) study of the schizeaceous spores of the Dakota Formation and other reconstructions that have emphasized the subtropical to tropical nature of the regional fossil assemblage (Rushforth 1971).

The precise community assignment for *A. lemonii* is more elusive. Agasie (1969), Rushforth (1971), and May and Traverse (1973) all suggested that the Dakota Formation was deposited on a wet, low-lying landscape in close proximity to drier uplands. The *Matonidium* leaf material occurs in an ash layer associated with a coal bed at the Westwater site. The swamps of the Dakota Formation, which produced the peat that is the original source of the coals of the region, apparently supported a diverse tree and shrub flora in which ferns were probable understory elements (Retallack and Dilcher 1981). In such situations, however, microtopographic variability can result in a complex vegetation mosaic with somewhat drier sites, possibly dominated by angiosperms, in close spatial assocation with the actual swamp vegetation. The coarser clastics of modern distributary channels and coastal lagoons usually include a mixed assemblage derived primarily from the lower coastal plain but also including wood that may have been transported for greater distances than is typically the case with the angiosperm leaves or conifer needles in such deposits. The coarser sandstone in which the specimens of *Agathoxylon lemonii* were collected suggests the possibility that they were transported from a well-drained habitat occurring somewhere along the lower delta plain associated with the deposition of the Dakota Formation.

ACKNOWLEDGMENTS

The authors wish to express their appreciation to S. R. Rushforth of Brigham Young University, Provo, Utah; S. R. Ash of Weber State College, Ogden, Utah; Greg Retallack of the Univesity of Oregon, Eugene, Oregon; and R. E. Taggart of Michigan State University, East Lansing, Michigan, for their review of the manuscript.

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GRAZING AND PASSERINE BREEDING BIRDS IN A GREAT BASIN LOW-SHRUB DESERT

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ABSTRACT.—Densities of passerine breeding birds were compared between four range pastures variously grazed by sheep over a 50-year period. The experimental pastures, located at the Desert Experimental Range in southwestern Utah, included three grazed and one ungrazed. Grazed pastures were each heavily stocked and grazed annually at one of three winter seasons (early, middle, or late). Important structural (physiognomic) and compositional differences existed in the vegetation of the experimental pastures. Horned Larks (*Eremophila alpestris* [Linnaeus]), numerically dominant in the pastures, apparently responded to those differences. Black-throated Sparrows (*Amphispiza bilineata* [Cassin]) and Loggerhead Shrikes (*Lanius ludovicianus* Linnaeus) were less common and found as breeding birds only in dry wash habitats. No significant differences were found between the pastures in estimates of total breeding bird populations, bird standing crop biomass, or bird species richness.

The low-shrub desert is a mosaic of plant communities found throughout the plains, foothills, and valleys of the Great Basin. In some areas, perennial grasses share dominance with the low shrubs. The desert has been variously classified as the shadscale association, the northern desert shrub formation, or the salt-desert shrub association (Holmgren 1973). Many of the native plants are palatable and nutritious, and the deserts are used primarily for winter grazing by domestic sheep (Holmgren and Hutchings 1972).

Physical environments of low-shrub deserts are rigorous. Climatically, they are cold deserts: winters are cold and summers are warm. Annual precipitation is generally low and occurs sporadically. Long-term irregularities in climatic patterns exist. The vegetation is structurally and floristically uncomplicated. Production rates are relatively low (Blaisdell and Holmgren 1984). These features of low-shrub desert environments and vegetation restrict avifaunal development to small species assemblages of broadly distributed forms (Wiens and Dyer 1975).

Vegetation structure is an important factor determining habitat selection in birds (reviewed in Hildén 1965). As a result, habitat structure may affect the organization of the avian community as a whole (Willson 1974, Roth 1976, Rotenberry and Wiens 1980). Because grazing can alter the structure of low-shrub desert vegetation (Hutchings and Stewart 1953, Holmgren and Hutchings 1972), different grazing treatments may have important consequences for avifaunal composition and abundance.

The objective of this study was to compare breeding bird populations and community organization between selected pastures variously grazed by sheep for 50 years. The study was restricted to passerine bird species.

DESERT EXPERIMENTAL RANGE

The study was conducted at the Desert Experimental Range in southwestern Millard County, Utah. It was established in 1933. Its 225 km^2 are representative of about 160,000 km^2 of winter grazing lands in the Great Basin physiographic province as well as adjacent parts of the Columbia and Colorado plateaus (Blaisdell and Holmgren 1984). About 75% of the Experimental Range is alluvial slope or flat valley bottom. The rest is steeper upland overlain by a shallow soil mantle and broken by ledges of hard Paleozoic sedimentary or Tertiary volcanic rock. There are no seeps, springs, or live streams. Numerous dry washes cross the alluvial fans and may flow for short periods following high-intensity summer showers. Elevation ranges from 1,547 to 2,565 m. Soil textures are typically loams, sandy loams, or loamy sands (Holmgren 1973).

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During the 50 years from 1934 to 1984, temperature extremes varied from −40 to 40 C. The ground is frozen most of the time from mid-November into March. Snowfalls are usually light, seldom more than 5 cm deep. The average annual precipitation is 15.7 cm, about half of which falls during the five months from May through September (Holmgren 1973).

The vegetation on the Experimental Range is a mixture of low shrub and shrub-grass types. The dominant shrub species are winterfat (*Ceratoides lanata* [Pursh] J. T. Howell), bud sagebrush (*Artemisia spinescens* D. C. Eaton in Wats.), and shadscale (*Atriplex confertifolia* [Torr. & Frem.] Wats.). Three perennial grasses—Indian ricegrass (*Oryzopsis hymenoides* [R. & S.] Ricker in Piper), galleta (*Hilaria jamesii* [Torr.] Benth.), and sand dropseed (*Sporobolus cryptandrus* [Torr.] Gray)—are associated with shrubs on most soils.

METHODS

Grazing studies began on the Desert Experimental Range during the winter of 1934–1935 (Hutchings and Stewart 1953). Sheep grazed 20 large (129 ha) range pastures at one of three intensities (light, moderate, or heavy) and one of three winter seasons (early, middle, or late). Grazing assignments for each experimental pasture remained unchanged. The winter of 1983–1984 marked 50 consecutive years of grazing in the pastures. The rest of the area was divided into 14 units. Over the years, 11 have been grazed by sheep and 2 by cattle. One unit had not been grazed.

Three heavily grazed pastures, one each grazed in early, middle, or late winter, and part of the ungrazed unit (hereafter referred to as the ungrazed pasture) were selected for study. The experimental pastures were chosen for maximal contrasts in seasonal grazing assignments and minimal differences in soil-site characteristics. Grazed pastures were contiguous, and all of the pastures selected for study were covered with similar plant types when the experiments started in 1934 (Hutchings and Stewart 1953). To avoid dissimilarities in soil and site characteristics, only the northern half of the late-winter grazed pasture and the eastern half of the ungrazed pasture were studied.

Four 9-ha plots were randomly located in each of the four selected experimental pastures and censused for breeding birds using the Williams spot-map method (International Bird Census Committee 1970). The square plots were surveyed and gridded in a Cartesian coordinate system with points flagged and numbered with stakes at 50-m intervals. Seven census visits were made to each plot from 5 April to 1 June 1984. Most of the work was done from sunrise to late morning. To ensure complete coverage, a plot was censused by walking within 25 m of all points on the grid. Census routes through each plot were varied. Observations extended well beyond plot boundaries.

At the end of the sampling period, concentrated groups of observations and coded activity patterns were circled as indicating areas of activity or approximate home ranges. Fractional parts of boundary territories were recognized. Results were converted to the number of pairs of breeding birds per 40 ha. Species richness (N) was expressed as the total number of breeding bird species observed on a plot.

Vegetation and other features of experimental pastures were measured from 11 June to 2 August 1984. A m^2 quadrat was located at each of 49 equally spaced stakes that defined the coordinates of the 9-ha bird census grids. Canopy coverage (Daubenmire 1959) was ocularly estimated for each plant species and recorded as the midpoint of one of eight percent coverage classes (0-1, 1-5, 5-10, 10-25, 25-50, 50-75, 75-95, and 95-100). Percentages of litter, rock, and bare ground were similarly estimated. Distances to the nearest grass plant, forb, and shrub in each quadrant were measured from the center of each quadrat. The patchiness of the vegetation was estimated using Roth's (1976) index of heterogeneity (D) calculated as

$$D = 100\,SD/\bar{x}$$

where SD is the standard deviation and $\bar{x}$ is the mean of the point-to-plant distances. The height of each grass plant, forb, and shrub nearest the center of each quadrat was measured with a pocket tape.

Vegetation data and attributes of avian community organization between experimental pastures were compared using analysis of vari-

TABLE 1. Vegetation and other features of grazed and ungrazed pastures, Desert Experimental Range, Utah, 1984.

Feature	Experimental pasture			
	Heavy, early winter	Heavy, middle winter	Heavy, late winter	Ungrazed
Ground cover (%)				
Bare ground	72.82 a	74.30 a	74.26 a	68.11 a
Litter	2.36 ab[1]	2.21 a	3.23 ab	4.49 b
Rock[2]	4.26 a	3.62 a	2.08 a	5.01 a
Grass				
Aristida purpurea	0.28 ab	0.02 a	0.02 a	0.93 b
Bromus tectorum	0.47 a	1.01 a	0.73 a	0.52 a
Hilaria jamesii	2.15 ab	0.42 b	0.95 b	3.66 a
Oryzopsis hymenoides	2.09 a	4.43 ab	10.19 c	4.82 b
Sitanion hystrix	0.17 a	0.13 a	0.02 b	0.64 c
Sporobolus contractus	0.04 a	0.58 ab	1.65 b	0.00 a
Sporabolus cryptandrus	6.51 a	5.25 ab	2.41 b	0.22 c
Others	0.02 a	0.00 a	0.00 a	0.21 a
Totals	11.73 a	11.84 a	15.97 a	11.00 a
Forb				
Chaenactis macrantha	0.02 a	0.05 a	0.00 a	0.05 a
Descurainia pinnata	0.01 a	0.00 a	0.00 a	0.10 a
Halogeton glomeratus	0.03 a	0.07 ab	0.25 b	0.29 ab
Lappula occidentalis	0.39 a	0.40 a	0.15 a	0.55 a
Lepidium montanum	0.20 a	0.45 b	0.02 c	0.06 c
Machaeranthera canescens	0.06 a	0.06 a	0.04 a	0.63 b
Phacelia corrugata	0.01 a	0.07 ab	0.00 a	0.18 b
Salsola iberica	0.02 a	0.03 a	1.54 b	0.10 a
Sphaeralcea grossulariifolia	0.59 a	0.19 b	0.23 b	1.10 c
Townsendia florifer	0.04 a	0.06 a	0.01 a	0.01 a
Others	0.10 a	0.33 a	0.04 a	0.19 a
Totals	1.47 a	1.71 a	2.28 ab	3.26 b
Shrub				
Artemisia spinescens	2.32 ab	1.22 a	0.02 c	2.53 b
Atriplex canescens	0.09 a	0.00 a	0.00 a	0.21 a
Atriplex confertifolia	3.94 ab	6.05 b	1.68 c	2.98 ac
Ceratoides lanata	2.49 a	0.84 b	1.10 ab	2.95 a
Chrysothamnus viscidiflorus	0.06 a	0.09 a	0.02 a	3.82 b
Xanthocephalum sarothrae	0.97 a	1.38 a	0.28 b	0.03 b
Others	0.50 a	0.51 a	0.23 a	0.07 a
Totals	10.37 a	10.09 a	3.33 b	12.59 a
Vegetation height (m)				
Grass	0.16 a	0.18 ab	0.23 c	0.21 bc
Forb	0.05 a	0.04 a	0.04 a	0.12 b
Shrub	0.11 a	0.12 a	0.12 a	0.15 a
Patchiness index (%)[3]				
Grass	107 a	107 a	116 a	120 a
Forb	109 ab	108 ab	122 b	89 a
Shrub	94 a	102 a	114 a	120 a

[1] Dissimilar letters in rows denote differences ($P < 0.10$) in means between pastures.

[2] Exposed bedrock and rock particles on the surface of the ground greater than 2.5 cm in diameter.

[3] Roth's (1976) index of heterogeneity.

ance for a 1-factor design. Multiple comparisons of means followed Gabriel (1978). Arcsin transformation was used for percentage data. Tests of significance were at $P < 0.10$.

Authorities for plant names are from Welsh et al. (1981). Bird nomenclature is from the 1983 AOU Check-list (American Ornithologists' Union 1983).

RESULTS

Vegetation

Structural and compositional differences existed in the vegetation of the experimental pastures (Table 1). The pasture grazed in late winter each year differed from the others mainly in its reduced shrub ground cover,

TABLE 2. Mean density (pairs/40 ha), standing crop biomass, and other attributes of passerine birds breeding on grazed and ungrazed pastures, Desert Experimental Range, Utah, 1984.

				Experimental pasture			
Species	Foraging category[1]	Nesting substrate[2]	Species weight[3] (g)	Heavy, early winter	Heavy, middle winter	Heavy, late winter	Ungrazed
Horned Lark (*Eremophila alpestris*)	GGO	G	31.3	19.7 a[4]	18.2 ab	14.9 b	17.8 ab
Black-throated Sparrow (*Amphispiza bilineata*)	GGO	B	14.0	7.9 a	9.6 a	4.3 a	4.6 a
Loggerhead Shrike (*Lanius ludovicianus*)	GFC	B	48.1	+[5]	+	0.4 a	0.8 a
	Total pairs/40 ha			27.6 a	27.8 a	19.6 a	23.2 a
	Total individuals/km^2			137.8 a	139.0 a	98.4 a	115.5 a
	Standing crop biomass (g/ha)			36.3 a	35.2 a	27.4 a	32.9 a
	Species richness (N)			2.0 a	2.0 a	1.7 a	1.5 a

[1] GGO = ground-gleaning omnivore, GFC = ground-feeding carnivore.
[2] G = ground nester, B = bush nester.
[3] Species weights from Schoener (1968), Rotenberry (1980), and Wiens and Rotenberry (1980).
[4] Dissimilar letters in rows denote differences ($P < 0.10$) in means between pastures.
[5] + indicates bird observed infrequently.

which was less than a third that of the other pastures. The reduced shrub cover and the slightly larger percentage of grass cover gave the late-winter grazed pasture a grassy aspect. Also, the average grass height was higher than those pastures grazed earlier in the winter. Bud sagebrush, common in the other pastures, was a minor part of the plant cover in the late-winter grazed pasture. Indian ricegrass dominated the grass component, and Russian thistle (*Salsola iberica* Sennen & Pau) was most abundant among the forbs.

Few features of the ungrazed pasture differed from those pastures that were grazed. The ungrazed area had slightly less bare ground and slightly more rock cover than grazed pastures, but neither component was significantly different from grazed pastures. There was significantly more litter cover in the ungrazed pasture when compared to the pasture grazed in the middle of the winter. Forbs made up a larger percentage of the ground cover and were taller in the ungrazed pasture. Of the more common perennials, squirreltail (*Sitanion hystrix* [Nutt.] J. G. Sm.), galleta, and globemallow (*Sphaeralcea grossulariifolia* [H. & A.] Rydb.) made up a larger percentage of the plant cover on ungrazed sites. Sand dropseed, common in grazed pastures, was a minor component in the ungrazed pasture. Among the shrubs, only low rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.) was more abundant in the ungrazed pasture.

The pastures grazed in the early- and middle-winter periods were comparable in nearly all the features measured. Only winterfat and globemallow had larger cover values in the early-grazed pasture; pepperweed (*Lepidium montanum* Nutt. in T. & G.) was more important in the pasture grazed in midwinter.

Birds

Only three passerine breeding bird species occurred in the experimental pastures (Table 2). The most common of these was the Horned Lark (*Eremophila alpestris* [Linnaeus]). A permanent resident, this broadly distributed bird was found throughout the variously grazed pastures. Less common, and found in more restricted habitats, were two summer residents, the Black-throated Sparrow (*Amphispiza bilineata* [Cassin]) and the Loggerhead Shrike (*Lanius ludovicianus* Linnaeus). Wide-ranging raptorial birds of prey, although commonly seen, were not included in the analysis. Large numbers of transient species were also excluded.

Mean breeding bird density ranged from 19.6 to 27.8 pairs/40 ha in the experimental pastures (Table 2). From 65% to 76% of the average total bird density in each pasture was accounted for by the Horned Lark. Black-throated Sparrow and Loggerhead Shrike numbers were highly variable. Among the individual species, only the Horned Lark differed significantly in density; the highest average density was in the early-winter grazed pasture and the lowest in the late-winter grazed pasture. Although not significant, there was a tendency toward intermediate bird density and bird biomass values in the ungrazed pasture. Species richness means were slightly higher in the early- and middle-winter grazed pastures. No significant differences were found in estimates of total bird numbers, bird standing crop biomass, or bird species richness between the various pastures.

DISCUSSION

Horned Larks were distributed throughout the experimental pastures. Few locations within the 9-ha bird census plots were not included within the territorial boundaries of a nesting pair of Horned Larks. Breeding territories were contiguous and frequently overlapped. Densities, however, differed between pastures. Horned Lark density was highest in the early-winter grazed pasture and lowest in the late-winter grazed pasture (Table 2). Important differences occurred in the floristics and the physiognomy of those two pastures (Table 1). The late-grazed pasture had the lowest shrub cover, the highest grass cover, and the tallest average grass height. Grasses, mostly Indian ricegrass, dominated the aspect. The early-grazed pasture had the lowest forb cover, the lowest average grass and shrub heights, and generally lower grass and shrub patchiness indexes. The visual impression was that of an open, low-growing, mixed grass-shrub habitat.

Black-throated Sparrows and Loggerhead Shrikes were locally distributed within the experimental pastures. As breeding birds, they were largely restricted to the dry washes that cross the alluvial fans and bajadas of the Desert Experimental Range. Dry washes were generally only a few meters wide, and they contained taller shrubs, mostly desert peachbrush (*Prunus fasciculata* [Torr.] Gray), interspersed among shorter vegetation. Densities of Black-throated Sparrows and Loggerhead Shrikes within the larger boundaries of an experimental pasture (Table 2) were apparently a function of the size and linear extent of the dry washes and the taller vegetation they contained.

The distribution of breeding birds within the experimental pastures is perhaps best explained by their different nesting requirements. Other investigators, working in a variety of habitats and locations, have noted the apparent preference of Horned Larks for open and low-growing vegetation as nesting sites (Fautin 1946, Wiens 1973, Owens and Myres 1973, Krementz and Sauer 1982, Castrale 1982). In this study, Horned Lark nests were found only in open habitats and always on the ground. Nests were placed in a shallow excavation partly beneath or beside a low shrub or grass tussock.

Fautin (1946) first noted that the Black-throated Sparrow seems to prefer an open type of vegetation within which there are occasional larger shrubs. Raitt and Maze (1968) found Black-throated Sparrows and Loggerhead Shrikes nesting exclusively in dry wash (arroyo) habitats. Similarly, I found Black-throated Sparrows and Loggerhead Shrikes nesting above the ground in the shrubs of the dry washes. Black-throated Sparrow nests were placed near the ground (<1 m) in small to medium-sized shrubs. Loggerhead Shrike nests were placed higher (>1 m) and in larger, more thickly foliaged shrubs.

Taller shrubs in the dry washes were frequently used as perches by each of the breeding bird species. Horned Larks sang from the ground, while perched, or from the air during nuptial flight displays. Black-throated Sparrows sang from elevated perches and sometimes foraged in the foliage of shrubs; they occasionally hawked insects from exposed perches. Loggerhead Shrikes used tall shrubs as observation posts. Both the Loggerhead Shrike and the Black-throated Sparrow were often seen coursing up and down the dry washes. Agonistic encounters between the two were occasionally seen in dry wash habitats. The Loggerhead Shrike was the aggressor in those encounters.

Several workers (e.g., Cody 1968, Wiens 1969, Rotenberry and Wiens 1980) have shown that the physical structure of the habitat can affect relationshps between grassland and shrubsteppe birds. In this study, significant structural differences were found in the vegetation of range pastures variously grazed by sheep for 50 years. One passerine breeding bird species, the Horned Lark, apparently responded to those structural differences. Other passerines, the Black-throated Sparrow and the Loggerhead Shrike, nested only in the taller vegetation that occurred in dry wash habitats. On the other hand, no significant differences were found in bird community attributes between the experimental pastures. The results of this study suggest that winter grazing by sheep, to the degree that it can alter the structure of low-shrub desert vegetation, has the potential to alter breeding bird populations and their distribution.

ACKNOWLEDGMENTS

I gratefully acknowledge the field assistance of G. Medlyn and J. Martin. J. Kinney, R. C. Holmgren, and W. P. Clary of the Shrub Sciences Laboratory at Provo, Utah, provided support and contributed in many other ways. J. Verner made constructive comments on an earlier draft of this manuscript.

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CHLOROPLAST ULTRASTRUCTURE IN THE DESERT SHRUB *CHRYSOTHAMNUS NAUSEOSUS* SSP. *ALBICAULIS*

Craig E. Coleman[1] and William R. Andersen[1]

ABSTRACT.—Ultrastructure of the chloroplasts of white rubber rabbitbrush (*Chrysothamnus nauseosus* (Pallas) Britt. ssp. *albicaulis*) was observed with electron microscopy. In addition, leaf anatomy was observed with light microscopy. Previously, it had been reported that the leaves of this desert shrub exhibited a relatively high rate of photosynthesis when compared to other C_3 plants. Comparisons with chloroplasts of other C_3 and C_4 plants demonstrated a reduced amount of granal stacking in the rabbitbrush. However, the classification of rabbitbrush as a C_3 plant is confirmed. RUBP-carboxylase concentration is reported at about 450 mg · ml^{-1} stromal space based on the estimation of 1 mg of chlorophyll per 25 ul of stromal space in a normal C_3 chloroplast and data from an assay to determine the ratio of RUBP-carboxylase to chlorophyll.

Recent interest in the desert shrub, *Chrysothamnus nauseosus* (Pallas) Britt. ssp. *albicaulis* (white rubber rabbitbrush), has led to a number of studies related to its ecology and physiology (McArthur et. al. 1979). Of particular interest has been its study as a nontraditional source of rubber. Ostler (1980) reported rubber acquisitions as high as 6% rubber per unit dry weight from the plant. As a result of this finding, studies are being conducted to discover some of the factors controlling the production of rubber. Recently work was done to determine some basic aspects of the photosynthetic characteristics of the plant. It was discovered that, under nonstressed conditions, white rubber rabbitbrush exhibits a relatively high rate of photosynthesis when compared to other C_3 plants (Davis et. al., 1985), and it was felt that an electron microscopic analysis of the chloroplast ultrastructure might shed some additional light on the problem. This paper, therefore, presents the result of this analysis, along with anatomical data obtained from light microscopy. Additionally, we report the approximate RUBP-carboxylase concentration in the stromal space based on an estimate for the concentration of chlorophyll in the stromal space.

MATERIALS AND METHODS

Leaves were removed from young branches of white rubber rabbitbrush plants growing in the greenhouse at Brigham Young University. The leaves were cut into sections approximately 1–2 mm long and placed immediately in 0.2 M sodium cacodylate buffered (pH 7.3) 2% glutaraldehyde 3% acrolein (v/v) solution for two hours for fixation. After being washed for one hour with a 1:1 solution of buffer and distilled water, the material was stained with 2% osmium tetroxide (w/v) diluted 1:1 with the sodium cacodylate buffer. The material was again washed with the buffer solution for one hour and subsequently dehydrated using an ethyl alcohol series.

The material was then embedded in Spurr's resin (Spurr 1969) by first rinsing three times in 100% acetone. It was allowed to stand for one hour each in first a 25% resin to acetone solution (v/v), then a 75% solution before finally embedding in 100% resin. Sections were obtained using a glass knife in a Porter-Blum MT-2 ultra-microtome. For electron microscopy, sections were mounted on copper grids previously coated with formvar and a light layer of carbon. Lead citrate was used as a poststain as previously described (Reynolds 1963). The sections were observed and photographed with a Phillips EM 400 transmission electron microscope. For light microscopy, sections were taken from the same resin-embedded material as used for electron microscopy. These sections were mounted on a glass slide and poststained with a 1% Toluidine Blue, 1% Azure II, and 1% $NaHCO_3$

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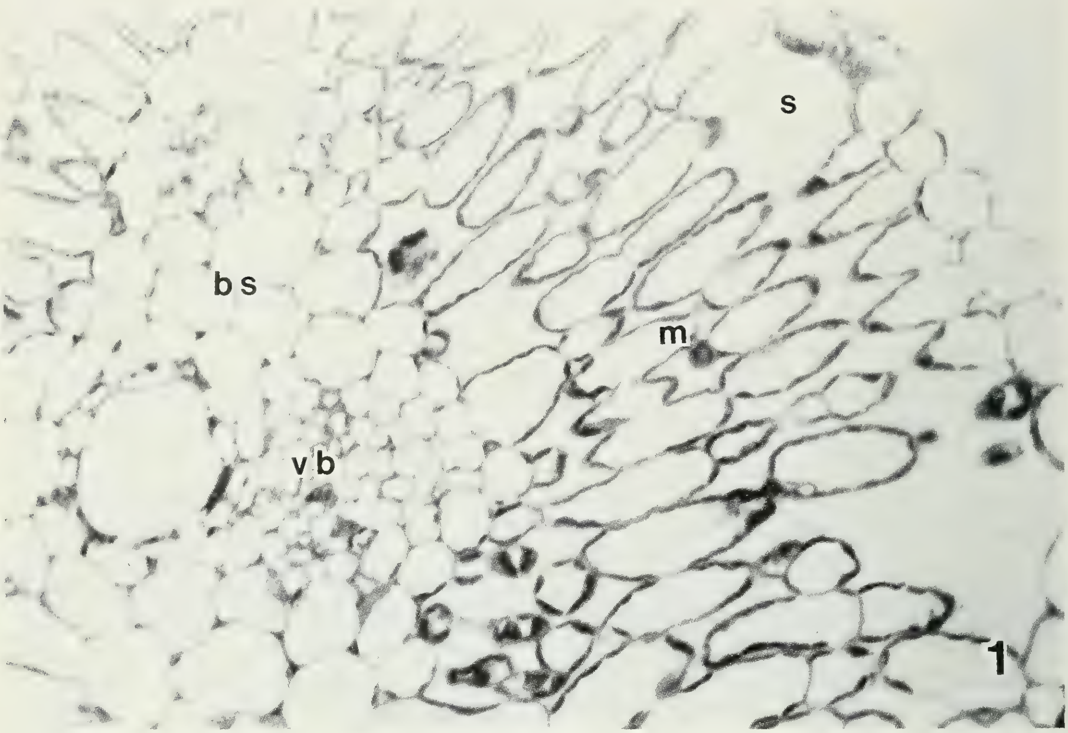

Fig. 1. Light micrograph of the transverse section of a rabbitbrush leaf showing bundle sheath cells (bs), mesophyll cells (m), stoma (s), vascular bundle (bs)(X170).

stain. An enzyme assay to determine the ratio of RUBP-carboxylase to chlorophyll was performed as described previously (Davis et. al. 1985).

RESULTS

LIGHT MICROSCOPY.—Transverse sections were viewed with the light microscope (Fig. 1) with the intent to compare the anatomy of the white rubber rabbitbrush with that of known C_3 and C_4 plants. Chloroplasts are located exclusively in the mesophyll cells and are lacking in the bundle sheath cells. This indicates the presence of C_3 metabolism (Laetsch 1974).

ELECTRON MICROSCOPY.—Typical chloroplasts observed with the electron microscope are shown in Figures 2 and 3. It should be noted that in all the chloroplasts observed there exsisted a uniformity of structure, in other words, a complete lack of dimorphism, which is usually exhibited in chloroplasts of C_4 plants (Laetsch 1968). Furthermore, chloroplast size and distribution do not seem to vary from one section of the leaf tissue to another.

The enzyme assay to determine the ratio of RUBP-carboxylase to chlorophyll in the chloroplast yielded a result of 11.24 ± 0.81 mg RUBP-carboxylase.

DISCUSSION

To determine if the chloroplasts of the white rubber rabbitbrush were unusual in any way, their ultrastructure was compared to the ultrastructure of the chloroplasts from several C_3 and C_4 plants reported in the literature. Thus, comparisons were made with chloroplasts from radish (Rufner et. al. 1984), barley (Robertson and Laetsch 1974), rye (Huner 1984), tobacco (Laetsch and Stetler 1965, Kasperbauer and Hamilton 1984), bean (Weier and Thomson 1962), rice (Miyake and Maeda 1976), spinach, and tomato (Rufner and Barker 1984). Although typical of C_3 anatomy, we note that the grana in the chloroplasts of the white rubber rabbitbrush seem to be less stacked in comparison to chloroplasts of mesophyll cells in both C_3 and C_4 plants. This, however, could be due to a variety of

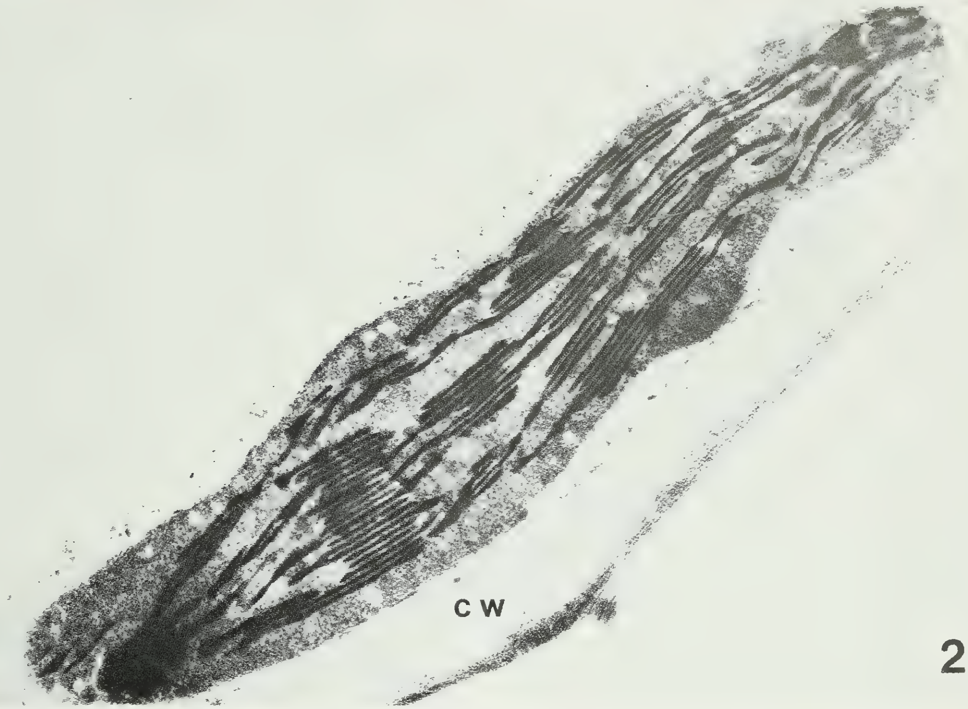

Fig. 2. Transmission electron micrograph of a rabbitbrush chloroplast lacking starch grains showing cell wall (cw)(X40,000).

factors, including the age of the leaf (Robertson and Laetsch 1974), the amount of light (Apel 1983), and the quality of light (Kasperbauer and Hamilton 1984) being absorbed by the leaves of the plants, or the absence of vital nutrients and mineral in the soil, such as iron (Rufner and Barker 1984). A most likely explanation for the reduced stacking is the age of the chloroplasts, since the leaves, although fully expanded, were taken from young shoots.

Heldt (1979) estimated the chlorophyll content in a normal C_3 chloroplast to be about 1 mg per 25 ul of stromal space. Data from an enzyme assay reported previously indicate the ratio of RUBP-carboxylase to chlorophyll in rabbitbrush to be 12.93 ± 0.74 mg RUBP-carboxylase $\cdot$ mg^{-1} chlorophyll (Davis et. al. 1985). This assay was repeated for the purpose of this paper and, as already stated, yielded a value of $11.24 + 0.81$ mg $\cdot$ mg^{-1}. Assuming Heldt's estimation of stromal space to be reasonable in this case, the concentration of RUBP-carboxylase in rabbitbrush chloroplasts is about 450 mg $\cdot$ ml^{-1}. This is a high concentration of the enzyme as compared to several other C_3 plants (values, on the average, are reported around 200–250 mg $\cdot$ ml^{-1}) (Ashton 1982, Kawashima and Mitake 1969; Lyttleton and Ts'o 1958; Molin et. al. 1982) and may be responsible for the increased rate of photosynthesis as observed in the plant.

ACKNOWLEDGMENTS

We wish to express gratitude to Dr. W. M. Hess and the staff of the Electron Optics Laboratory for their assistance in completing the microscopy for this paper.

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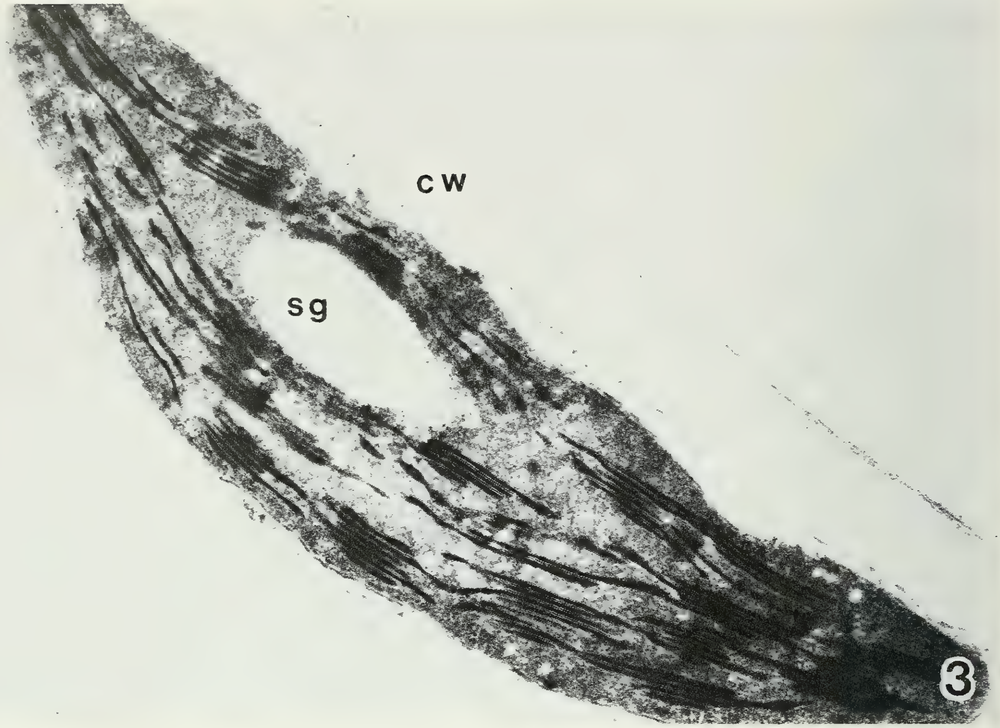

Fig. 3. Transmission electron micrograph of a rabbitbrush chloroplast with a prominent starch grain showing cell wall (cw), starch grain (sg)(X45,000).

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GENETIC VARIATION OF WOODRATS (*NEOTOMA CINEREA*) AND DEER MICE (*PEROMYSCUS MANICULATUS*) ON MONTANE HABITAT ISLANDS IN THE GREAT BASIN

William T. Mewaldt[1,2] and Stephen H. Jenkins[1]

Abstract.—Seventeen loci were examined for polymorphism in four populations of *Neotoma cinerea* and *Peromyscus maniculatus* on isolated mountain ranges in the Great Basin, one population of each in the Sierra Nevada, and one of each in the Rocky Mountains. All *Peromyscus* populations had higher levels of heterozygosity than syntopic *Neotoma* populations. Results

cate; interstriae 1 moderately elevated, very slightly higher than interstriae 3, with a median

Populations of species restricted to terrestrial habitat islands may be similar to those on oceanic islands in patterns of gene frequency change over time (Kilpatrick 1981). For example, Glover et al. (1977) studied pikas (*Ochotona princeps*), which are generally restricted to talus slopes and other rocky habitats at high elevations. Their findings of low heterozygosity within populations are consistent with patterns on oceanic islands reviewed by Soule (1976) and Kilpatrick (1981), who concluded that the stochastic processes of founder effect and genetic drift may cause unpredictable shifts in gene frequency and reduced heterozygosity. The distribution of montane habitats in the Great Basin of the western U.S. provides an opportunity for "island-mainland" comparisons of montane mammals. In the Great Basin, isolated patches of forested habitat act as refugia for many populations of mammals that apparently cannot live in or cross the intervening deserts (Brown 1971). As recently as 8,000 years ago, climatic conditions were such that forests (interspersed with pluvial lakes) existed continuously across the Great Basin from the Sierra Nevada to the Rocky Mountains. Since that time, the climate has become drier, resulting in isolation of montane habitat at higher elevations of the mountain ranges (Wells 1983). We analyzed allozymes in several populations of two cricetid rodent species, *Neotoma cinerea acraia* (Elliot) (bushy tailed woodrat) and *Peromyscus maniculatus sonoriensis* (LeConte) (deer mouse), to test some genetic predictions of the hypothesis that stochastic effects should be more pronounced for isolated island populations than for "mainland" populations. *Peromyscus maniculatus sonoriensis* is distributed continuously across the Great Basin (Hall 1946), whereas *Neotoma cinerea acraia* is found in isolated populations on most of the Basin ranges (Brown 1971).

Biochemical variation within at least 20 species of *Peromyscus* has been reported (e.g., Selander et al. 1971, Kilpatrick and Zimmerman 1976, Zimmerman et al. 1978, Avise et al. 1979, Gill 1980). Of special interest here are the studies by Avise et al. (1979) and Gill (1980), both of which included *P. m. sonoriensis*. Avise et al. reported mean heterozygosity ($\bar{H}$) values for populations of this subspecies ranging from 0.074 to 0.124, whereas Gill found an H of 0.118.

Electrophoretic studies of *Neotoma* are few. Mascarello (1978) studied three chromosomal races of *Neotoma lepida* in the southwest but did not report $\bar{H}$ values, whereas Zimmerman and Nejtek (1977) reported $\bar{H}$ values for three semispecies of *Neotoma* (*N. albigula*, *N. micropus*, and *N. floridana*) in southern North America ranging from 0.024 to 0.140, with an average of 0.078. Heterozygosity measures for populations of *N. cinerea* have not been reported.

Materials and Methods

Six mountain ranges with populations of *N. c. acraia* and *P. m. sonoriensis* were chosen

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TABLE 1. Allele frequencies for polymorphic loci of *Neotoma cinerea* and *Peromyscus maniculatus*, and mean heterozygosity per locus over all loci sampled ($\overline{H}$).*

Population	Sample size	ES-B	ES-C	AAT-1	GDH	PGD	$\overline{H}$
			Neotoma cinerea				
Sierra Nevada (Carson Range)	16	100	100	100 (.93) 120 (.07)	84 (.04) 100 (.96)	100	0.013
Shoshone	17	82 (.025) 100 (.975)	100	100 (.80) 120 (.20)	84 (.05) 100 (.925) 118 (.025)	92 (.025) 100 (.975)	0.034
Toiyabe	14	100	94 (.18) 100 (.82)	100 (.93) 120 (.07)	84 (.21) 100 (.79)	100	0.046
Toquima	15	100	94 (.07) 100 (.93)	100 (.87) 120 (.13)	84 (.10) 100 (.90)	100	0.033
Snake	14	100	100 (.93) 104 (.07)	100 (.77) 120 (.23)	100 (.97) 118 (.03)	92 (.03) 100 (.97)	0.037
Rocky Mountains (Tushar Range)	15	100	94 (.31) 100 (.69)	100 (.97) 120 (.03)	100	100	0.030

Population	Sample size	ES-A	ES-C	AAT-1	GDH	LDH-2	PGD	$\overline{H}$
				Peromyscus maniculatus				
Sierra Nevada (Carson Range)	18	100 (.91) 118 (.09)	100 (.74) 106 (.26)	100 (.76) 120 (.24)	89 (.15) 100 (.85)	100	100	0.075
Shoshone	15	100 (.97) 118 (.03)	100 (.63) 106 (.27) 110 (.10)	100 (.77) 120 (.23)	100 (.97) 111 (.03)	100	100	0.064
Toiyabe	15	100 (.97) 123 (.03)	100 (.73) 102 (.03) 106 (.20) 110 (.03)	100 (.67) 114 (.10) 120 (.23)	89 (.13) 100 (.70) 111 (.17)	100	83 (.13) 100 (.87)	0.108
Toquima	18	100 (.94) 118 (.06)	100 (.58) 106 (.39) 110 (.03)	100 (.53) 120 (.47)	89 (.14) 100 (.80) 111 (.06)	100	83 (.14) 100 (.83) 112 (.03)	0.112
Snake	21	100	100 (.64) 106 (.34) 110 (.02)	100 (.57) 120 (.41) 138 (.02)	89 (.045) 100 (.91) 111 (.045)	91 (.02) 100 (.98)	83 (.02) 100 (.98)	0.079
Rocky Mountains (Tushar Range)	13	100 (.96) 118 (.04)	100 (.81) 110 (.19)	100 (.65) 120 (.35)	89 (.08) 100 (.92)	100	100	0.064

*Alleles designated according to proportional electrophoretic mobility relative to the most common allele (100). Frequencies given in parentheses. $\overline{H}$ calculated according to formula (3) in Nei (1978), for 17 scorable loci for *Neotoma* and 16 scorable loci for *Peromyscus*.

for analysis (Table 1). All mountain ranges are over 80 km long and have peaks of over 3,000 m. Animals were collected in the summers of 1978 and 1979. Total sample sizes were 91 for *N. c. acraia* and 100 for *P. m. sonoriensis* (Table 1).

Techniques of tissue (liver and kidney) preparation and enzyme staining for all loci except esterases were modified from Selander et al. (1971) and Gabriel (1971). Esterase analysis using napthol-AS-D-acetate as a substrate followed Van Deusen and Kaufman (1978). All electrophoresis was done in polyacrylamide slab gels, with both homogeneous and gradient type gels run in a water-cooled Pharmacia electrophoresis tank. Use of polyacrylamide rather than starch gels permitted better resolution of separate bands for some loci, such as the esterases.

In all, seventeen presumed loci were analyzed for each species. These included carboxylesterase (ES-A, ES-B, and ES-C; E.C. 3.1.1.1), phosphoglucomutase (PGM; E.C. 5.4.2.2), malate dehydrogenase (MDH-1 and MDH-2; E.C. 1.1.1.37), malate dehydrogenase (oxaloacetate-decarboxylating) ($NADP^+$)

TABLE 2. Genetic distances* between pairs of *Neotoma cinerea* populations (above diagonal) and pairs of *Peromyscus maniculatus* populations (below diagonal) on mountain ranges in the Great Basin.

	Sierra Nevada	Shoshone	Toiyabe	Toquima	Snake	Rocky Mountains
Sierra Nevada		.00043	.00263	0	.00107	.00532
Shoshone	0		.00316	0	0	.00711
Toiyabe	.00093	.00288		.00034	.00409	.00262
Toquima	.00401	.00473	.00240		.00022	.00387
Snake	.00217	.00093	.00331	0		.00645
Rocky Mountains	.00258	.00236	.00371	.00793	.00477	

*Formula for genetic distance (D) from Nei (1978).

(MDH-3; E.C. 1.1.1.40), cytosol aminopeptidase (CAP; E.C. 3.4.11.1), L-lactate dehydrogenase (LDH-1 and LDH-2; E.C. 1.1.1.27), glucose dehydrogenase (GDH; E.C. 1.1. 1.47), isocitrate dehydrogenase (NADP$^+$) (IDH; E.C. 1.1.1.42), aspartate aminotransferase (AAT-1 and AAT-2; E.C. 2.6.1.1), xanthine dehydrogenase (XDH; E.C. 1.1.1.204), phosphogluconate dehydrogenase (PGD; E.C. 1.1.1.43), and superoxide dismutase (Sod; E.C. 1.15.1.1). Choice of enzymes for analysis was based on our ability to obtain reproducible and unambiguous results from among those enzymes listed and studied by Selander et al. (1971). Enzyme nomenclature and E.C. numbers are from Moss (1982) and International Union of Biochemistry (1984).

RESULTS AND DISCUSSION

Twelve of the loci analyzed were monomorphic in *Neotoma* and 10 were monomorphic in *Peromyscus*. For both species, the same allele was fixed in all 6 populations at each of the monomorphic loci. Five loci were polymorphic in one or more populations of *Neotoma*; 7 were polymorphic in one or more populations of *Peromyscus* (Table 1). Esterase-B was so variable in *Peromyscus* that it could not be scored accurately; this locus is omitted from Table 1.

Extremely low interpopulation genetic distances, D (Nei 1978), and proportionately large standard errors showed no clear patterns in either species (Table 2). The mean D was 0.0028 for all pairs of *P. maniculatus* populations and 0.0025 for all pairs of *N. cinerea* populations. There was no significant correlation between genetic distance and geographic distance for either species ($r = 0.48$ for *N. cinerea*, $0.05 < P < 0.10$; $r = 0.12$ for *P. maniculatus*; $P > 0.50$).

Heterozygosity ($\overline{H}$) was significantly greater for *P. maniculatus* (mean for the 6 populations = 0.084) than for *N. cinerea* (mean = 0.032; $P = 0.03$ by randomization test for matched pairs). The difference between species would be even greater if we had not excluded the highly variable ES-B locus from calculations for *Peromyscus*. Heterozygosity values were greater for all the central Great Basin populations of *N. cinerea* than for either the Sierra or Rocky Mountain population. The same was true for all but one of the *P. maniculatus* Great Basin populations (Table 1).

Our results in general are not consistent with the expectation that gene flow should be less and genetic drift greater for *Neotoma cinerea* populations than for *Peromyscus maniculatus* populations on isolated mountain ranges in the Great Basin. One or both of two factors could account for this inconsistency. First, *N. cinerea* populations might not be as isolated in montane habitats on Great Basin ranges as we initially assumed. Indeed, *N. cinerea* are occasionally captured below the lower tree line in some parts of Nevada (Hall 1946, personal observations). Sufficient interpopulation gene flow could forestall genetic divergence. Second, the populations studied may have been too large or the time since isolation of their forested habitats too short for measurable genetic drift to have occurred.

Our finding of significantly greater heterozygosity for populations of *P. maniculatus* than for the syntopic populations of *N. cinerea* is consistent with a general pattern of greater genetic variablity of *P. maniculatus* than is found in most other rodent species that have been examined (Smith et al. 1978, Avise et al. 1979, Smith 1981). The niche-width variation hypothesis (Nevo 1978) might account for this pattern, since *P. maniculatus* is more generalized in both diet and habitat than *N. cinerea* and many other rodents. The high reproductive rate of *P. maniculatus* may also contribute to its ability to maintain relatively high levels of heterozygosity (Smith 1981).

Populations of *N. cinerea* and *P. maniculatus* on isolated mountain ranges in the Great Basin were generally more heterozygous than populations in Sierra Nevada or Rocky Mountain sites. The latter sites were near the range limits for both *N. cinerea acraia* and *P. maniculatus sonoriensis*, the subspecies which were used in our study (Hall 1981). McClenaghan and Gaines (1981) documented greater genetic variability for central than for marginal populations of *Sigmodon hispidus*; our results exhibit a similar pattern at the subspecific level.

Although our initial predictions were not verified for the particular populations we studied, the Great Basin system of terrestrial habitat islands seems to be well suited for testing a variety of hypotheses about mammalian populations genetics. The paleoecology of this area is well understood (Wells 1983), which provides a good foundation for such studies.

ACKNOWLEDGMENTS

We thank the University of Nevada Research Advisory Board for financial support, W. Welch for assistance with electrophoresis, and A. Gill, D. Hafner, and W. Welch for comments on the manuscript.

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BREEDING RECORDS FOR CLARK'S GREBE IN COLORADO AND NEVADA

Richard L. Bunn[1]

ABSTRACT.—Described as a new breeding species is Clark's Grebe in Colorado and Nevada.

The Western Grebe (*Aechmophorus occidentalis*) and Clark's Grebe (*A. clarkii*) were originally named and described by Lawrence (1858 in Baird 1858) as two species based on plumage, bill structure, and color, and size. Coues (1874) reduced the Clark's Grebe to subspecific rank, which was upheld by the American Ornithologists' Union (*in* Nuechterlein 1981). Recently, a decision by the AOU Committee on Classification and Nomenclature (AOU 1985) restored the Clark's Grebe to specific rank, based on studies of assortative mating (Storer 1965, Ratti 1979), spatial segregation (Ratti 1979), and, within sympatric populations, advertising calls and ecological segregation (Nuechterlein 1981). Breeding populations of Clark's Grebe are known in Oregon, California, Utah, North Dakota, and South Dakota in the United States; Manitoba and Saskatchewan in Canada; Chihuahua, Durango, Zacatecas, Nayarit, Jalisco, Michoacán, Guanajuato, San Luis Potosi, State of Mexico, and Guerrero in Mexico (Storer 1965, Ratti 1979, 1981, Nuechterlein 1981, Williams 1982). This note reports the nesting of Clark's Grebe in Colorado and Nevada.

Two courting pairs of Clark's Grebe were observed 21 June 1978 at Barr Lake, Adams County, Colorado (B. Andrews, personal communication). Since then Clark's Grebe has been sighted in small numbers in eastern Colorado in the South Platte River drainage. They are apparently far less abundant there than the Western Grebe during migration and during the nesting season (personal observation). However, in the Arkansas River valley and areas in the San Luis Valley, the Clark's Grebe represented approximately half or more of the breeding *Aechmophorus* grebe population on several reservoirs from 1983 to 1985.

On 4 July 1983 Charles Chase III and I found 20 adult and 5 juvenile Clark's Grebes in Saguache County, Colorado, southwest of Russell Lakes State Wildlife Area. Four juveniles occurred singly and were each accompanied by one adult bird; one juvenile was accompanied by two adults. The grebes were seen on two reservoirs that had extensive bullrush stands along their western edge. The advertising calls of the Clark's Grebe were heard throughout the visit, but Western Grebes were neither seen nor heard on either reservoir.

On 17 June 1984 I saw 33 adult and 8 juvenile Clark's Grebes at Stillwater National Wildlife Refuge, Fallon, Nevada. The juveniles occurred singly with either 1 or 2 accompanying adults on Lead and Goose lakes. Only adult Clark's Grebes were seen on Stillwater Point Reservoir.

ACKNOWLEDGMENT

I thank Bob Andrews for the early records of Clark's Grebe in Colorado and Diana F. Tomback, Charles Chase III, and Steve Bissel for helpful criticisms of the manuscript.

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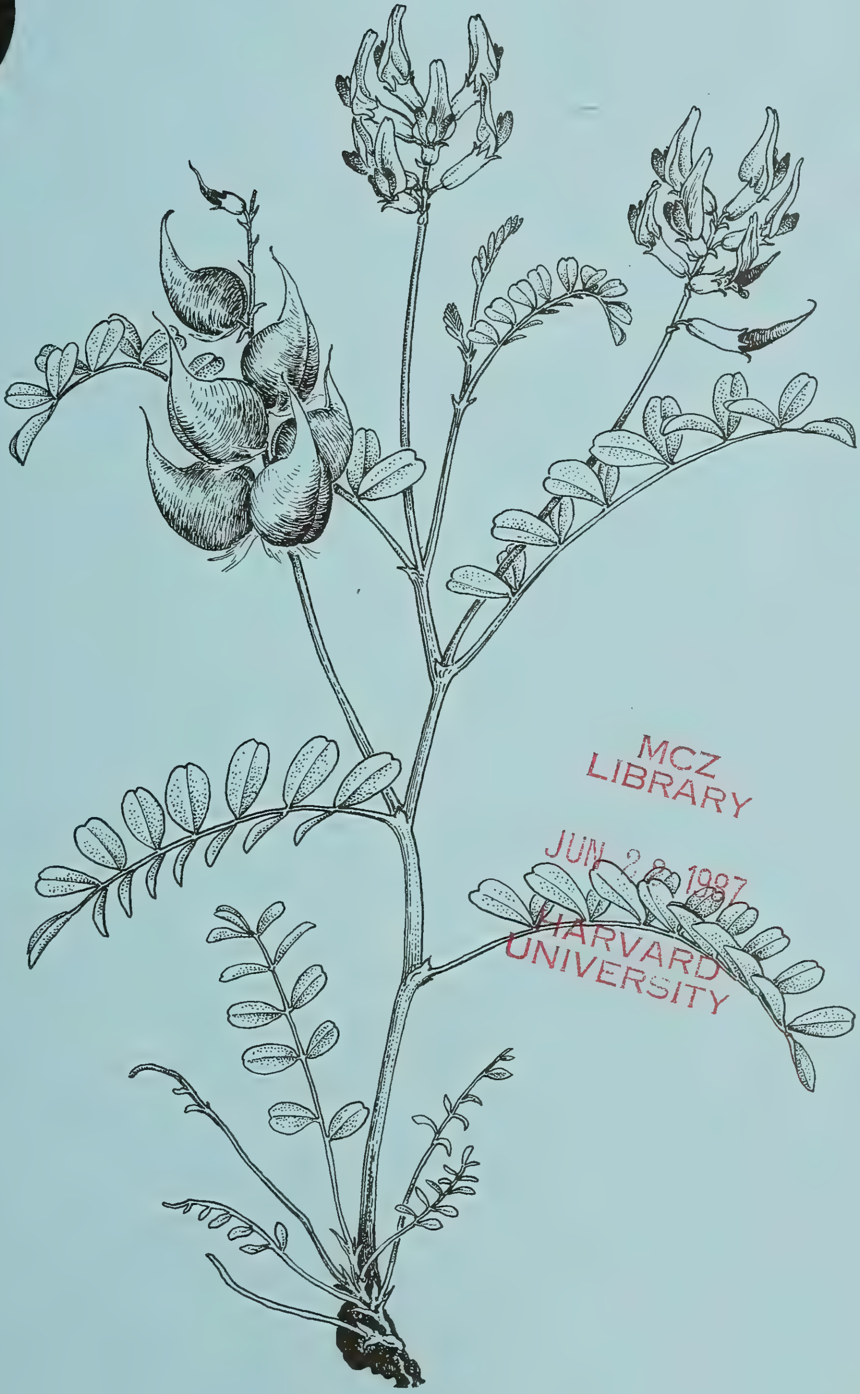
me 46 No. 4 31 October 1986 Brigham Young University



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3-87 650 28024

ISSN 017-3614

The Great Basin Naturalist
PUBLISHED AT PROVO, UTAH BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 46 31 October 1986 No. 4

HISTORY OF FISH HATCHERY DEVELOPMENT IN THE GREAT BASIN STATES OF UTAH AND NEVADA

J. W. Sigler[1] and W. F. Sigler[1]

ABSTRACT.—Fish hatchery systems in both Utah and Nevada are now an integral part of the fishery management scheme. Historic development of hatcheries, including the early stocking of exotics, is presented. Disease control and dry pelleted feed are discussed in historical perspective and present status.

Waters in the Great Basin area were probably first fished by wandering bands whose ancestors had crossed the Bering Strait to Alaskan shores and subsequently inhabited a vast portion of what is now the western United States. These people were present on the shores of ancient Lakes Bonneville and Lahontan about 8,000 to 10,000 years ago. Recently published archaeological evidence indicates, however, that these people were not the direct ancestors of the Pyramid Paiute Indians who now inhabit the area surrounding Pyramid Lake, the remains of ancient Lake Lahontan, nor of the Indians found near Great Salt Lake by explorers in the early 1800s. These Indian tribes had been preceded by people of the Desert Culture as early as 10,000 years B.P. (before present) (Sigler and Sigler 1987).

EARLY HISTORY

When great numbers of white men arrived in the valleys of the Great Basin from 1847 to 1870, the streams and lakes in the area supported large populations of native fishes. Utah, Sevier, and Bear lakes in Utah, and Pyramid, Walker, and Tahoe lakes in Nevada, as well as the major streams of the basins (the Bear, Weber, Logan, Blacksmith Fork, Ogden, Jordan, Provo, and Sevier rivers in Utah, and the Truckee, Carson, Humboldt, and Walker rivers in Nevada), supported substantial numbers of native cutthroat trout, *Salmo clarki*, as well as endemic suckers, whitefishes, and chubs (minnows). These populations were essentially unexploited, in the present-day sense of the word, by the nomadic Indians who utilized them. Harvests of the fish during the spawning runs each year provided the Indian tribes with subsistence diets for much of the year. Some trading of excess fish occurred among the tribes and the early white explorers and trappers, but the fish populations were never endangered by the Indians.

The influx of whites in 1859 in Nevada following the discovery of the Comstock Lode, and the arrival of the Mormon pioneers in Utah in 1847, however, exerted heavy pressure on the fish populations in both states. The easily harvested fish, present by the thousands during spawning runs, became an integral part of the diet of the settlers near major lakes and streams of the Great Basin (Townley 1980, Yarrow 1874, Madsen 1910, Carter

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1969). Methods used to harvest fish included the use of "giant powder," dams, nets, and traps. At the same time, changes in water use patterns (for irrigation and industry) began to adversely affect the fish populations. Streams were blocked, and large numbers of mature fish were taken prior to spawning. Young-of-the-year fish were lost to irrigation canals. As a result, populations of native fish in some areas were drastically reduced. Additionally, the native populations were threatened by the unregulated introduction of nonnative species of fish into many of the waters of the Great Basin.

Initial Fish Stockings

In both Utah and Nevada, early fish introductions were made primarily for the purpose of increasing the food supply in the territories. This encouraged a wide and somewhat unstructured program of stocking whatever species were available. Prior to, or in some cases concurrent with, the development of "hatching stations," exotic species were distributed throughout the easily accessible waters of the two states.

Common carp, *Cyprinus carpio*, was one of the most frequently introduced fish. It was brought into the United States in 1876 by Rudolph Hessel (Hessel 1878). Utah received its first shipment of carp from the Washington, D.C., U.S. Fish Station in 1881, when 130 adult carp were distributed in five Utah counties and H. G. Parker, the first Fish Commissioner of Nevada, in his biennial report to the governor in 1878, expressed his intent to stock the waters of that state with this "superior food fish."

Over the next several years, thousands of carp were planted in streams in Utah and Nevada, sometimes as many as 17,000 annually. The shipments into Utah continued until 1903, and intrastate stockings from established populations persisted for several more years. In Nevada the stocking of carp continued until 1889, when George Mills became the third fish commissioner. Mr. Mills made public his sentiment concerning carp in his report to the governor, stating:

> Several years ago, during the carp furor, the general government, while not entirely to blame, was "particept criminis" in foisting upon this state, and in polluting our waters with, that undesirable fish, the carp. True, application for some were made by many of our citizens ignorant of the qualities and habits of the fish and unsuspecting as to the ruin their introduction would bring. Time has now established their worthlessness, and our waters are suffering their presence. As a food fish they are regarded inferior to the native chub and sucker, while their tenacity to life and everlasting hunger gives them a reputation for "stayers and feeders" unheard of in any fish reports I have seen to date. A resident of Humboldt, an "old Humboldter" informs me they have not only devoured all the fish food in the Humboldt River, but also the duck food and a band of sheep grazing along the banks.

Carp are now present at lower elevations in all the major drainages in Utah (Popov and Low 1950, Sigler and Miller 1963) and in Nevada (Miller and Alcorn 1945, La Rivers 1962).

HATCHERY DEVELOPMENT IN UTAH

The Period 1850–1900

In 1856 Utah's Deseret Agricultural and Manufacturing Society strongly supported fish planting programs. Salt Lake City raised capital to create the first private hatchery in the area by selling shares in the venture. Spawners (presumably cutthroat trout) were procured from the headwaters of the Weber River and from Utah Lake, and eggs were hatched.

Albert Perry Rockwell, warden of the Utah Territorial prison from 1862 to 1871, used prisoners to raise fish at what is now 2525 South 1100 East in Salt Lake City, Utah. Rockwell received more than 100,000 "salmon" eggs from the hatchery at McCloud River in California between 1877 and 1879.

The need for a state hatchery in Utah was first documented in the 1894 fish and game commissioner's report to the legislature. Joseph Musser, Fish and Game commissioner, stated:

> fish can be artificially multiplied almost indefinitely at very nominal cost. It is a great pity that Utah has not a liberally endowed hatchery system. Other states and territories have each from one to eight or ten public or private hatcheries. . . . From a well equipped hatchery, millions of choice fry could be annually distributed. This would mean thousands of dollars for the good of the territory.

In his 1897–98 report, John Sharp, Utah State Fish and Game warden, notes that distribution of trout (plantings) has been "comparatively insignificant to what it should be and will necessarily continue to be so until a state hatchery is established and provision made for the stocking of our numerous mountain streams." During this period, thousands of fry, chiefly brook trout (*Salvelinus fontinalis*) obtained from the federal government, and black spotted or cutthroat trout were held in ponds, primarily in Parley's Canyon, until they were planted, generally in the spring.

The first state-controlled hatchery-type areas involved the closing of streams, one in each county. Commissioner Sharp states in his 1898 report:

> The reservation or the closing of one stream, lake or pond, in each county for the purpose of planting and propagating trout with which to stock other streams, is in my opinion, a very good provision, which will undoubtedly result in considerable benefit to the fish interests of the state in helping to restock the mountain streams.

Ten streams were reserved in 1897 in different parts (counties) of the state. Each stream was closed for varying periods of time, generally three or four years. Sharp notes, however, that "there remains much necessity for a state hatchery with capacity to hatch from one million to two million trout fry per year to be placed in the streams of the state." He also points out that this would benefit not only the residents of the state but, in concert with protection for game in the mountains, would become an alluring attraction for tourists, health seekers, and sportsmen of other states, resulting in considerable revenue for the state. Sharp urged the legislature to appropriate funds for the construction and maintenance of a state hatchery.

Utah's third biennial report of the Fish Commissioner is dated 1900. In it, Commissioner Sharp states that a legislative act has provided for the establishment and maintenance of a state fish hatchery. The commissioner was to supervise all fish culture matters of a public nature and to receive and care for the food fishes and ova that came into the possession of the state. He was to obtain fry and/or ova in such variety as he deemed most suitable to the waters of the state and to distribute them to the waters in an approved and equitable manner. He was empowered to furnish, at cost, to any person, corporation, or company owning any lake or reservoir as private property, the young or fry hatched in the state hatcheries. The commissioner also had a mandate to examine the waters of the state that were not naturally stocked with fish to determine their suitability for fish. He was then to stock them with the most suitable varieties of fish. Five thousand dollars was appropriated for the commissioner's use in carrying out these duties.

The site of the first hatchery was evaluated on the basis of its quantity and quality of water, having a constant temperature of 50 F and being free from all foreign matter. The availability of additional spring or creek water was also required for use in the rearing ponds. Sites were examined in Cache, Box Elder, Weber, Morgan, Summit, Juab, Utah, and Salt Lake counties. A site in Salt Lake county, 1.5 miles east of Murray, at the junction of two spring creeks known as "the spring runs" was selected. After 5.75 acres of land were purchased by the governor at a cost of $1,000, the hatchery was constructed at a cost of $922. It began operation 30 December 1899.

The first hatchery houses in Utah and Nevada were similar. Each consisted of wooden troughs, about 14 feet long, 14 inches wide, and 6 to 10 inches deep. Each trough could hold approximately 50,000 eggs.

Throughout this period, thousands of brook trout were distributed to public waters and private citizens in both states with the understanding that the commission retained access to the ponds and reservoirs for the purpose of taking eggs and fry.

The concept of "branch hatcheries" was discussed at this time. The idea was to hold fish at various locations to reduce long hauls. In addition to activating "branch hatcheries," rearing ponds were used to supplement the capacity of the hatchery rearing facilities.

The Period 1901–1920

In Utah this period was characterized by increasing awareness of the needs of the fish being hatched in the state hatchery and of the importance of stocking adequate numbers of fish in designated streams. Brook trout were extremely successful in many habitats, particularly the Logan River and the lakes in Big Cottonwood Canyon, which was producing seven-pound fish within six years. Utah's hatchery doubled its production in the first few years of this period, mostly because of the use of black-spotted trout eggs from Fish Lake. More than 2,000,000 eggs were processed in both 1901 and 1902. The establishment of a brood stock at the state hatchery also contributed to its success.

The use of "hatching ponds" began in 1902, when land north of Nephi was given to the state for use as a fish-rearing pond.

A private hatchery was started near the town of Mantua by J. S. Hull in 1906. (The general area of this hatchery was purchased from Beatrice Foods by the Utah Division of Wildlife Resources in 1973 and is now the site of the division's Bear Lake cutthroat trout hatchery.)

When the need for additional hatchery space became evident, the 1909 Utah legislature authorized the construction and operation of three additional hatcheries. One hatchery was constructed near Springville, one at Fish Lake, and one at Panguitch Lake. State hatchery capacity for hatching eggs subsequently reached 12,000,000. Also in use at this time were large ponds near the Telluride Power Plant on the Provo River. These ponds were used to hold black-spotted trout spawners migrating from Utah Lake.

Powell Slough, 4 miles north of the mouth of the Provo River on the shore of Utah Lake, was designated as the "bass hatchery" for the state, providing an ideal location and water supply for the rearing of this species. Some 3,000,000 or more fish were hatched annually during the next several years.

Between 1900 and 1905 the Murray Hatchery was producing in excess of 3,000,000 trout eggs per year in a hatchery designed for only 2,000,000. Approximately 18,000 brood fish were maintained at this hatchery, which provided fry throughout northern Utah. The Springville Hatchery maintained 10,000 brood fish and, in a hatchery designed to produce 2,000,000 eggs, was rearing 2,500,000 fry for stocking in Utah Lake and the central part of the state. The Panguitch Hatchery was used to hatch eggs from the Murray Hatchery and did not maintain a brood stock because of the prohibitively low temperature of its water. Fish from this hatchery were stocked in Panguitch Lake and the extreme southern part of the state.

By 1914 Utah no longer maintained domestic brood stock of brook trout but utilized brown trout, *Salmo trutta*, and rainbow trout, *Salmo gairdneri*, exclusively. Both brook and native (cutthroat) eggs were obtained from wild stocks from streams. At the same time, 2,000,000 brook trout and 4,000,000 cutthroat trout eggs were obtained from spawning stations at Fish Lake, Provo River, Panguitch Creek, and Puffer's Lake each year.

Success rates in hatching brown trout eggs were noted at 80% for this period. The most important aspect of rearing fry from eggs was providing them with proper food and feeding conditions. Finely ground beef livers were used predominantly. Careful feeding, several times per day, resulted in a 95% survival of the hatch to two-inch fingerlings in six weeks.

Costs of fish food rose rapidly during the war years of 1917–1919, and brood stocks at Utah hatcheries were reduced to conserve funds. Motor vehicles replaced teams of horses for stocking as a money-saving effort and provided the additional benefit of being faster.

In the fall of 1917, the federal government established a hatchery at Springville with the stipulation that a fair percentage of the spawn taken from state waters would be returned as fry.

The Period 1921–1940

Brood stock in Utah hatcheries had been reduced because of the high cost of fish food during World War I. By 1921–22, this situation had reduced the production capacity of the Utah hatcheries, and it was decided to rebuild the brood stock and expand hatchery production capacity in response to increased public demand for additional stocking of Utah waters.

During this period and earlier, ground and canned carp was the principal fish feed. Canned carp mixed with low-grade flour produced exceptional growth, and the fish were free of gill infection problems. In the two-year period of 1928–1930, the state canned 160 tons of carp for fish food at a cost of less than 4 cents per pound. Cooperative efforts with such organizations as the Salt Lake County Fish and Game Protective Association and the Logan, Ogden, Vernal, Roosevelt, Duchesne, and Beaver fish and game associations boosted fish production by means of the state providing the fish and fish food, and the associations furnishing the care and rearing facilities.

As of 1924 Utah operated seven hatcheries: Logan, Murray, Springville, Timpanogos, Whiterocks, Glenwood, and Beaver. In excess of 17,000,000 fish were being raised at these hatcheries. Another hatchery constructed in 1926 on the headwaters of the Sevier River had a capacity of 2,500,000 fish per biennium.

Roy Hull operated a private hatchery at Mantua for 11 years from 1928 to 1939 and then operated a private hatchery in Murray, Utah, for E. C. Bennett. This hatchery was closed in 1948 because of the growth of Salt Lake City. The required city wells were depleting the hatchery water supply.

In 1948, Roy Hull moved his operation (Clearview) to a site in Provo Canyon that provides ideal rearing temperatures, 58 F with 2-degree annual fluctuation. Because of the temperature, which is unsuitable for eyeing eggs, Clearview currently purchases 200,000 Kamloops eggs annually. The Clearview Trout Farm now produces about 50,000 pounds of trout per year as food fish that are distributed throughout the western states. As with all private hatcheries, it is inspected and certified by the state.

Fry (fish less than 2 inches long) had been routinely stocked by most of the western states from the inception of their hatchery programs. By 1928 Utah had begun to also stock fingerling extensively along with larger fish, believing that better survival was achieved with the larger fish in many waters.

Prior to 1924 the stocking of fish in both Utah and Nevada, particularly at locations distant from the hatcheries, had been by 10-gallon milk cans on light trucks. This method of stocking fish was extremely expensive and limited the numbers of fish that could be transported in a single trip. Specially designed fish-planting trucks were constructed to alleviate this shortcoming. Utah's first modern trucks consisted of 150-gallon tanks with oxygen supplied under pressure and cooled with ice. This advance in planting techniques resulted not only in 75% reduction in stocking costs, but it also insured that the fish arrived at their destination in better condition.

In 1929 federal funds were made available for investigations of fish habitat in mountain lakes and streams of the west. Dr. Vasco M. Tanner, Brigham Young University, led the effort in Utah, compiling information on more than 70 lakes in the Uinta Mountains. Each lake was studied with regard to its size, depth, temperature, spawning area, etc. Recommendations as to species, size, and number of fish to be stocked were included in the reports.

The Period 1941–1970

Although funding was restricted during the years immediately preceding the involvement of the United States in World War II, existing hatcheries were maintained and some new facilities were constructed in Utah under the federal WPA program.

By 1956 Utah was operating 12 hatcheries. These hatcheries provided rainbow trout, brown trout, brook trout, lake trout, *Salvelinus namaycush*; largemouth bass, *Micropterus salmoides*; walleye, *Stizostedion vitreum vitreum*; and unnamed salmon. Most of the fish stocking was by insulated tank trucks equipped with water pumps and oxygen systems, but some areas were planted using pack horses and airplanes. Hatchery production was becoming increasingly necessary to satisfy public demands. This necessitated changes in the hatchery system. Manufactured dry food capable of growing rainbow and other trout from fry to catchable size, without meat supplement, was developed at the Glenwood Hatchery by June Powell, Clark Feed Company, Purina, and others. This reduced the cost of fish per pound and substantially increased production. The use of irrigation reservoirs as "natural" rearing areas for fry proved successful, allowing small fish to be stocked inexpensively in the spring, and seven-inch "wild" fish to be removed in the fall for stocking. Additional rearing facilities were added to many of the state hatcheries along with expanded water supplies. Ten production hatcheries are now operating in Utah: Fountain Green, Glenwood, Kamas, Loa, Midway, Mantua, Panguitch (now Mammoth Creek), Springville, Whiterocks, and J. Perry Egan. Total annual capacity is now 8,663,000 fish weighing 788,000 pounds.

Fish were reared to 8 to 10 inches in a move to provide fishermen with larger fish. Stream surveys, funded by Dingell-Johnson, were completed on many of Utah's waters.

HATCHERY DEVELOPMENT IN NEVADA

The Period 1875–1900

Nevada's Commissioner Parker had, in 1878, utilized a "hatching house" for some 250,000 McCloud River "salmon" (possibly rainbow trout) spawn. Parker's report for 1881–82 indicates the need for "means to hatch and distribute the fish provided free by the General Government in Washington, D.C." This is probably the first official statement of Nevada's requirement for a hatchery system more elaborate than hatching trays.

W. N. Carey, Nevada's fish commissioner from 1885 to 1889, took the first structured steps toward developing a hatchery system and propagating fish for stocking. The hatching house used by Parker had evidently been his private property and, upon assuming the duties of fish commissioner, Carey used "such tanks and other appliances as found in the presence of his predecessor and belonging to the State." A hatchery house was constructed on Carey's property in Carson City, Nevada. In his 1885–86 report to the governor, Carey documented the need for a state-owned and controlled facility, stating that the cost would be approximately $500. Carey's 1887–88 report noted that the State Hatching House "is running to its full capacity," so construction must have been approved. During this same period, a brook trout egg-taking facility was established at Marlette Lake with the cooperation and aid of J. B. Overton, superintendent of the Virginia and Gold Hill Water Works.

George Mills became fish commissioner in 1889. His 1889–90 report to the governor states the "State Hatchery was unfitted (sic) for the work required and that he was forced to provide a more suitable building." He outfitted the new facility, expending $250 for fittings and plumbing and $300 for the transfer of state property to the new facility.

Mills, in his 1891–92 report, notes an attempt to establish a branch hatchery at Elko. However, he "entertained doubts as to the supply and temperature of water for hatching eggs." He therefore planted 140,000 trout eggs in the Humboldt River.

The Period 1901–1920

In 1905 the Nevada Legislature created a three-man State Fish Commission. The commission members soon realized that if the waters of the state were to be adequately stocked, additional hatching and rearing facilities were required. In 1907 ground was obtained for the Verdi Hatchery, and construction was completed in 1909. Nevada then hired its first Fish and Game employee to operate the Verdi facility. Eggs from the Carson City Hatchery were transferred to Verdi, and the Carson City facility was relegated to being an egg-eyeing station.

Between 1911 and 1920, the commission continued to hatch and distribute fry of several species of fish. New buildings to better facilitate egg and fry handling were completed at the Verdi Hatchery in 1912. A private hatchery authorized in White Pine County was operated successfully by Mr. E. L. Fletcher of Ely. Additional permits for hatcheries were granted to individuals or groups in Verdi and Reno after the requirements of the permits had been met and the areas inspected by state personnel.

In August 1916 the Carson City Hatchery was closed as an economic measure and all operations previously conducted there were transferred to the Verdi Hatchery. Attempts to hatch brook trout taken from Marlette Lake were continually plagued by unacceptable (low) water temperatures at the Verdi Hatchery. In 1919 a facility constructed at Lakeview, Washoe County, to handle all aspects of the brook trout culture proved very successful. The field station at Numana (on the Pyramid Lake Paiute Indian Reservation), which had been built to take spawn from Lahontan cutthroat trout, *Salmo clarki henshawi*, was operated on an annual basis and collected eggs from Lahontan cutthroat trout and rainbow trout. Rainbow trout eggs were also collected from spawners taken at the Reduction Works Dam on the Truckee River near Reno.

Throughout this period hatchery superintendents and the Nevada Fish Commissioner regularly remarked on the need for additional space or facilities in the hatchery system. An additional complaint of the fish commissioners of both states was the lack of proper screening on the canals and the lack of fish ladders on diversion dams. These two problems, coupled with industrial pollution, caused the loss of thousands of fish. It was estimated that 40% of the fish planted were lost to irrigation canals. A proposal was made to increase license fees to pay for screening of the canals on the major rivers. The solution, however, was long in coming.

The Period 1921–1940

Ground horse meat and beef liver were used as a fish food at this time, allowing greater quantities of feed to be readily obtained. Other than routine problems associated with weather and water supplies, the Nevada hatcheries were operated at full capacity during most of this period, stocking thousands of fingerling and larger fish.

The Period 1941–1970

Fishery surveys and efforts to map the water resources of the state were conducted between 1941 and 1970 in Nevada to "determine the food productivity and physical conditions for use in future management . . . and to determine the stocking needs of the counties." An extensive survey of the lower Truckee River was planned, and stream improvement projects, including the screening of all principal diversions in the Truckee, were proposed.

In the 1950–52 biennial report of the Nevada Fish and Game Commission, Director Frank Groves reported that hunting and fishing license purchases had reached staggering proportions, increasing from 61,207 in 1947 to 82,492 in 1951. He further stated that surveys in the neighboring states showed that for each dollar invested in a hunting or fishing license, $50 was spent in pursuit of hunting or fishing. Expanding these figures, he estimated a value in excess of $314,000,000 for the fish and wildlife resources of the state. These figures did not include the monetary outlays of the people who used the waters and lands of the state for recreation other than hunting and fishing.

Thomas J. Trelease, the first chief of fisheries for Neveda, developed management policies and fish stocking programs for state waters. These policies dictated how fish from the federal hatcheries at Hagerman, Idaho, and Springville, Utah, as well as those reared by state facilities, were to be used and distributed. It was decided that the state hatcheries would rear fish to either 1 inch or 1.5 inches for transport to the rearing stations, where they would be raised to approximately a 6-inch length. Surplus fingerlings from the hatcheries would then be distributed to the various counties.

The Period 1970–Present

In 1981 the Nevada Department of Wildlife operated five fish propagation facilities: the Verdi Hatchery at Verdi, the Washoe Rearing Station at Reno, the Gallagher Hatchery at Ruby Valley, the Spring Creek Rearing Station at Baker, and the Lake Mead Hatchery at Lake Mead. Total capacity was 400,000 pounds yearly.

Summary—Hatcheries

A general public awareness of the need to conserve resources as well as to eliminate pollution in water, air, and soil surfaced early in the 1970s. Whereas much benefit was gained by this new involvement of the public, the state hatcheries continued to experience restrictions on growth brought about by inflation.

Both Utah and Nevada now operate hatchery systems to satisfy, to the best possible extent, the demands of the fishing public. As new reservoirs are created, additional warm water or cool water fish production will be required. Hatchery programs will continue to play an important role in fisheries management and be prepared to expand to meet increasing public demands for stocked fish.

Hatcheries in both states have evolved from rather small, primitive "hatching houses," which served only to hatch eggs, into large sophisticated stations that maintain and produce large numbers of fish of several species of various sizes. Fish hatcheries are now an integral part of the management plans of both states.

HATCHERIES AND FISH DISEASES

Two aspects of hatcheries in the Great Basin deserve discussion in light of the effect they had on hatchery management in Utah and Nevada. Disease control and the use of dry pelleted feed drastically altered hatchery operations in both states and elsewhere in North America.

Diseases in fish hatcheries can be broken into three categories: (1) historical aspects, (2) evolution of understanding, and (3) prevention and control: current status historical aspects.

Historical descriptions of diseases affecting fish originate at least as early as 330 B.C., when Aristotle described a crustacean parasite of tuna and swordfish (Post 1983). Fish cultural activities by the Chinese have included investigation and treatment of disease for several centuries.

Scientific descriptions of numerous diseases were written in Europe as early as the latter part of the 19th century. Among these were such titles as "On Vegetable Structures Found Growing in Living Animals: Parasitic Fungi in Living Animals," Transactions of the Royal Society of Edinburgh by J. H. Bennett in 1844, and "Notes on the Salmon Diseases in the Esk and Eden," Transactions of the Botanical Society of Edinburgh, Volume 13, by Brook in 1879. Additional contributions included T. H. Huxley's 1882 paper, "A Contribution to the Pathology of the Epidemic Known as 'Salmon Disease'," Proceedings of the Royal Society of London, Volume 33, and T. Huxley's 1882 article, "*Saprolegnia* in its relation to an epidemic in salmon," Quarterly Journal of the Microbiological Society, Volume 22. In the first three decades of the 20th century, there was information on and descriptions of diseases and its effects.

North American historical information is rather sketchy prior to 1946. Several fish culturists, however, treated visible diseases of fish with salt, acetic acid, copper sulfate, potassium permanganate, lime, calcium hypochlorite, formalin, and other disinfectants. An additional treatment or means of control for pathogenic organisms in fish hatcheries was the complete drying out of the hatchery. This necessitated stopping all production for a period of up to two years. Although actual recognition of diseases (and their agents) was quite slow in developing, some recognition of disease mechanisms did occur. Livingston Stone first recognized the secondary infection characteristics of the fungus infections of fish eggs in 1872. Seth Green's dropsy, or blue-swelling, white spot of eggs and fry, blue patch deformities, and pin-headed conditions were given as causes of losses of fry. L. Stone, who was particularly interested in fish diseases, described 23 diseases on the basis of symptoms or known causes, attributing at least some of them to poor nutrition. He held that identifying the cause and describing the symptoms were the first steps in the discovery of cures. Stone also determined that some fish diseases could be treated by either salt or other mechanisms (Bowen 1970). It is interesting to note that Stone's first choice for disease treatment was to improve the environment, either by increasing water flow or reducing the number of fish, thus reducing crowding and stress. Additionally, he treated diseases with a liberal application of fresh earth to the trough containing sick fish. Although most fish diseases were not recognized as being caused by specific agents or pathogens, early fish culturists in North America did realize that the fish were sick or in distress and were in some cases able to treat or at least mitigate that distress. Treatment by reducing the amount of crowding (pond loading) is still effectively utilized today.

The principal limitations to effective disease control prior to 1946 included: (1) lack of understanding of factors and causative agents, (2) lack of effective drugs and/or other treatment chemicals, and (3) poor understanding of disease-spreading mechanisms.

In the early part of the 20th century, fish culturists became aware of the relationship between epizootics of fish and loading levels in rearing facilities. Relationships between overcrowding and infections of opportunistic bacteria, fungi, and animal parasites were noted. Treatment for most diseases of fish was limited to use of various disinfectants, closing of the fish hatchery, or stocking diseased fish into streams and lakes, a practice prevalent during the early 1900s (Post 1983).

Evolution of Understanding

Following World War II the increased manpower and research monies available for all aspects of fish culture, including disease control, led to a rapid accumulation of both quantitative and qualitative information on not only the causative agents of fish diseases but of the mechanisms of disease spread and infection. Frederick Fish, H. S. Davis, S. Snieszko, and R. Rucker, and associates of these individuals, started producing what became an immense body of information regarding fish diseases. The establishment of the Eastern Fish Disease Laboratory at Leetown, West Virginia, and the Western Fish Disease Laboratory in Seattle, Washington, were two centers where tremendous effort produced information regarding fish diseases. These laboratories pioneered the collection and publication of descriptive, qualitative information regarding numerous diseases of fish, providing an information base. With this information in hand, Snieszko and others proceeded to establish information dissemination channels to federal and state fish culturists. In the late 1950s, the U.S. Fish and Wildlife Service began their fish cultural schools, including a warmwater one at Marion, Alabama, and the coldwater one at Cortland, New York (started by Abe Tunison), which is now the Tunison Fish Nutrition Laboratory. All federal hatchery superintendents or hatchery managers were required to attend the Cortland school. Stan Snieszko and other experts started training courses at Leetown and Seattle. Those individuals with interest and potential were selected to then complete the one-year Leetown disease school courses. Individuals who had completed both of these one-year training courses then became troubleshooters for hatcheries and initiated programs to work with biologists in solving fish disease programs. Many regional fish disease biologists were then available. Eventually this group became the diagnostic arm of the Fish and Wildlife Service's fish culture program. Emphasis at this time in the program was on diseases, nutrition, and the development of hatchery management programs. Diagnostic methods as well as chemotherapeutic treatment techniques were developed. State programs were initiated and state personnel were trained at Leetown, starting in the early 1960s. The basic emphasis at this time was to apply the acquired knowledge to the treatment of diseases.

In the early 1960s an unofficial network among fish pathologists and fish culturists developed. This was utilized to alert state and federal personnel when fish with known diseases were to be shipped to other locations. At the same time, development of improved methods for shipping both live fish and eggs (particularly salmonids) were developed. This had the effect of changing what had been local problems to a collection of substantial disease problems that were being spread from one state to another. Populations that were immunologically inexperienced were exposed to pathogens from other geographic areas, often resulting in complete destruction of existing populations, either wild or in hatcheries. Treatment technology at this time was extremely expensive, and in many cases the disease organisms were nonresponsive to available treatments (e.g., the sulfas in treatments of furunculosis). At this time the development of antibiotics and nitrofurans started but had the unfortunate result of being utilized to treat diseases as a method for increasing hatchery production. The diseases were not being eradicated but were rather suppressed by the chemotherapeutic treatments; thus the problem was not solved but simply masked (Goede 1985).

The concept of environmental stress and its relation to disease was more clearly elucidated in the early 1960s and subsequently resulted in efforts to reduce both the development and spread of diseases in hatcheries by better hatchery management practices. This came to include such things as pond loading indices based on water turnover rates, available dissolved oxygen, and crowding factors. At about the same time in the United States the federal Food and Drug Administration (FDA) and later the Environmental Protection Agency (EPA) began to restrict drugs and other treatments that could be utilized on hatchery fish that were going to be stocked and potentially consumed by humans.

Prevention and Control: Current Status

California was the first state to instigate border inspections of fish and fish eggs shipped into the state, but no federal legislation exists to date. The efforts to obtain federal legislation have involved at least eight legislative bills introduced into both houses of Congress. Each has failed to pass (Post 1983). The primary reason federal legislation has not been passed is that it must be umbrella legislation dealing with everything from tropical fish to catfish to the trout industry, plus mariculture enterprises. This includes such marine products as lobster and shrimp. No legislation acceptable to all parties has yet been proposed.

Utah has had a state inspection system since 1967. Since that time all shipments of eggs entering the state for the production of brood stock or other use are inspected and certified as "disease-free" before the shipment is accepted or allowed into the state. The Division of Wildlife Resources Fisheries Experiment Station at Logan, Utah, was constructed in 1962 and has been involved in the fish inspection effort since its introduction. A brood stock program was started in Utah in 1967, and once the brood stock had been certified as disease-free, it was transferred to the Egan state hatchery, near Bicknel (Goede 1985). At this time other states in the West were accepting shipments of eggs that were not certified disease-free simply because they required larger numbers of fish than they could produce. The conflicts resulting from some states accepting noncertified eggs or fish versus those that would accept only certified eggs or fish eventually resulted in a request that blocks of states devise a uniform policy for handling disposition and movement of diseased stock. In 1971 the Colorado River Wildlife Council was authorized to develop a basin disease control plan. The council is composed of the four states of Nevada, Wyoming, Colorado, and Utah in the upper basin, and the three states of Arizona, New Mexico, and California in the lower basin. The appointed delegates to the first meeting, which was held in Page, Arizona, were to establish a disease policy that would be in effect in all seven states. This policy, which was submitted by the advisory group in 1972, went into effect in January 1973. Recommendations of the council were ratified by each of the fisheries agencies and became state policy. Features of this agreement were enforced through respective state statutes. The policy was designed to prevent shipment into the Colorado River drainage of any fish, fish eggs, or fish products that had not been certified as disease-free. In Utah the policy does not cover only Colorado River waters, but all waters of the state. This policy has been incorporated into Utah and Nevada proclamations that govern import and movement of fish, fish eggs, etc. This was unquestionably a significant event in disease control in the Colorado River Basin and within the states of Utah and Nevada. All fish-rearing stations in the Colorado River drainage are now inspected and certified. In addition, any fish eggs or live fish that are moved into the drainage must be certified. This includes (in addition to state-controlled hatcheries) all private hatcheries within the basin. Permits must be acquired to import stocks of fish for any use whatsoever within the boundaries of the Colorado River Basin, and the stocks must have a valid certification inspection by a recognized professional fish pathologist using acceptable techniques.

The certification program of the Colorado River Basin has been followed by comparable programs for the Great Lakes area. The Columbia River drainage states are presently working to define a similar policy.

Assisting the efforts for certification and inspection of fish stocks before they are moved from one geographic area to another has been the ad hoc Fish Disease Committee of the American Fisheries Society that was formed in 1964. The Fish Disease Committee encourages fish disease control and fish health in general. Among the efforts of the committee was an annually published list of the diseases of most interest. Voluntary restriction of movement of fishes exposed to these diseases was urged on an international, interprovince, and interstate basis (Post 1983). These efforts assisted in the development of the United States Fish and Wildlife Service Title 50 "Restrictions on Movements of Certain Food or Sport Fishes from Countries which have Pathogens Unknown in Fishes in the United States." This restriction became effective in 1969 and was followed by similar Canadian legislation in 1971. The Fish Disease Committee was replaced by a Fish Health Section in the American Fisheries Society in 1972. The Fish Health Section advocates certification of fish health specialists by an examining board and has prepared a publication on standardized disease diagnostic procedures. Additionally, the Fish Health Section strongly encourages colleges and universities to provide courses of training for fish health specialists (Post 1983).

In both Utah and Nevada, specific programs within the fish and wildlife agencies can be directly attributed to efforts to control the spread of fish diseases. The establishment of the Fisheries Experiment Station at Logan, Utah, in 1962 is a direct effort by Utah to provide expertise, information, and methodologies for controlling and preventing both the outbreak and the spread of diseases in fish hatchery and wild populations. One aspect of disease control that has effectively reduced the outbreaks of disease in fish cultural stations in both Utah and Nevada is the utilization of various methodologies for achieving stress reduction. Generally speaking, pathogens can be present in fish populations with no apparent disease symptoms, and as long as the fish populations are not stressed and depression of the inflammatory response does not occur, the presence of the infectious agent may be of little consequence. However, high densities of fish in rearing facilities allow the transmission of infection, both horizontally (transmitted from one fish to another or to other organisms) and vertically (transmitted from parent to progeny) and must be regulated following currently accepted methodologies of pond-loading densities. In situations where diseases occur, environmental stress that is a direct precursor to the outbreak can generally be pinpointed and removed. In Utah chemotherapeutic agents have not been used more than five or six times since 1972 (Goede 1985). This is the result of more effective hatchery management. At present only a handful of diseases (principally viruses) that are transmitted vertically persist in Utah fish populations. These diseases are considered untreatable. It is these diseases that the current legislative statutes encompass in the inspection and certification program that is designed to prevent movement into currently certified disease-free populations.

DRY PELLETED FOOD

Since early efforts to propagate and raise fish artificially, hatchery managers have recognized the need for large amounts of food that is nutritionally balanced and provides necessary proteins, fats, minerals, and vitamins. In the late 1940s and early 1950s, prior to the advent of dry pelleted feeds (mid- to late 1950s), a diet referred to as a Cortland No. 3 diet was used extensively in many hatcheries. Only in the last three decades has the need for a complete, nutritionally sound diet been recognized. Research into more specific requirements for fats, protein levels, vitamins, amino acids, and other constituents is ongoing in an effort to improve production for several cultured species.

Utah, at one time, fed thousands of pounds of cornmeal and lesser amounts of fresh ground carp. An example of the amount of feed needed for one hatchery was provided by Red (John) Hansen (personal communication 1985). The Red River Hatchery in Questa, New Mexico, had a standing contract for 15,000 pounds of boned horse meat a month. One horse provided 250 to 300 pounds of usable meat, thus requiring 50 horses a month (600 a year) per hatchery. There were soon few available horses. The problems, cost, and nutritional inadequacies of fresh meat diets led to efforts to develop a manufactured dry (less than 10% moisture) feed that was nutritionally sound.

A load of dry feed from a manufacturer on the east coast was shipped to New Mexico in 1953 but was found to be lacking in nutritional qualities. This finding led to efforts to develop an acceptable dry feed. Early in 1953 Mr. J. R. Clark, a poultry nutritionist in Albuquerque, New Mexico, was contacted as a potential supplier of dry feed by the New Mexico Game and Fish Department. Initially, experimental diets for fry and fingerling were developed and tested at the New Mexico Red River Hatchery. These feeds were than taken to Arizona (Page Springs Hatchery), Utah (Glenwood Hatchery), and Colorado (Rifle Creek Hatchery) to be tested under varied environmental conditions. By 1956–57, several feed mills were producing dry feed. Currently several mills in the western United States produce a nutritionally sound trout diet. In other areas of the country, dry feed is produced for warm water species.

Early results of the feed tests were better than expected, and a technique for monitoring red blood cell count was employed to track nutritional changes in test fish. The greatest problem encountered early on was convincing hatchery personnel that fish would grow well, if not better, on one-half the weight of feed required with previous feeds. By 1956 dry feeds were being utilized in several states, and large-scale experimental feeding programs were underway.

Currently most feed manufacturers produce three different diets for trout: the fry diet, for fish up to about 2.5 inches long; a crumble diet for fish up to 4.5 to 5 inches long; and a pelleted diet for large catchable or market-size fish (8 to 10 inches long). There is considerable variation between these diets, principally in the content of protein and fat.

One new technology developed in Europe and used in the United States since about 1978 is spray fat application. Normally fat content of dry pelleted food is limited in content by the tendency of fat-saturated (8%) feed to crumble. Spray application allows use of 14% fat. Food conversion rates are also much higher. Historically a 2:1 feed:weight gain ration has been considered good. Presently most hatcheries achieve 1.5:1 and some are as high as 1.09:1. (By comparison, cattle are 8:1.) A pound of trout can now be reared for $0.30 to $0.35.

The complexity of dry diets for trout is impressive, and although improvements are constantly being made, the basic components are well established and documented. These ingredients are documented in the U.S. Fish and Wildlife Services Open Formula Diet. Nutrient requirements for cold water species are listed in a National Academy publication, one of a series on nutrient requirements of animals.

The Morgan Hatchery (now closed) was evidently the first Utah Hatchery to regularly feed dry feed. In 1954 the hatchery used dry food, along with meat products fed intermittently.

Utah's state hatcheries now utilize 670 tons of dry feed annually, and commercial users purchase another 1,250 tons. Nevada's state hatcheries purchase 570,900 pounds of dry feed annually.

ACKNOWLEDGMENTS

We thank Thomas J. Trelease, Chief of Fisheries of Nevada (retired); John King, Nevada Department of Wildlife; Bruce Schmidt, John Leppink, and Ron Goede, Utah Division of Wildlife Resources; Roy Hull, Clearview Trout Farm; Don and Chris Nelson, Murray Elevators; Jack Coates, Makah Tribal Council; and Larry Lee and Red (John) Hansen, Moore-Clark Company, for input and review of various sections of this article.

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COMPOSITION AND ABUNDANCE OF PERIPHYTON AND AQUATIC INSECTS IN A SIERRA NEVADA, CALIFORNIA, STREAM

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ABSTRACT.—The species composition of periphyton and benthic insect communities and abundances of common taxa (>0.1% of individuals) were examined during snow-free months in Convict Creek, a permanent snowmelt- and spring-fed stream in the Sierra Nevada of California. The communities were highly diverse. The most abundant taxa in the periphyton were diatoms (*Achnanthes minutissima, Cocconeis placentula lineata, Cymbella microcephala, C. sinuata, Fragilaria construens, F. crotonensis, Navicula* spp., *Synedra acus*, and *S. rumpens*), except in late spring and summer when several seasonal blue-green algae (*Chamaesiphon incrustans, Lyngbya* spp. and *Oscillatoria* spp.) are at their maximum densities. Most common periphyton taxa vary systematically in abundance with season, but relative abundances of taxa also appear to be influenced by streambed scouring and by concentrations of ambient nutrients.

Data on population densities and length frequencies of larval and nymphal stages of common benthic insects and occurrences of pupal and adult stages were examined to determine life history patterns. Taxa hatching in winter and spring and abundant as immatures in late spring include ephemeropterans (*Epeorus longimanus, Drunella flavilinea*, and *Caudatella heterocaudata*), plecopterans (*Calineuria californica, Doroneuria baumanni*, and *Pteronarcys princeps*) and dipterans (*Cryptolabis* sp.). Common taxa hatching in late spring or summer are the plecopteran *Malenka* (*californica?*) and the trichopterans *Arctopsyche grandis* and *Rhyacophila acropedes*. Several bivoltine and multivoltine ephemeropterans (*Baetis devinctus* and *B. tricaudatus*) and dipterans (*Simulium* spp. and Chironomidae) have summer cohorts. Taxa hatching in late summer or autumn and most abundant in autumn include ephemeropterans (*Baetis* spp., *Ephemerella infrequens, Epeorus dulciana, Ironodes lepidus*, and *Paraleptophlebia pallipes*), trichopterans (*Hydropsyche oslari, Lepidostoma* spp., *Glossosoma califica, Micrasema* sp., *Brachycentrus americanus, Neophylax* sp., and *Rhyacophila vaccua*) and dipterans (*Antocha monticola, Pericoma* sp., and Chironomidae). Major recurring events that may influence life history patterns and structure of the benthic insect community are (1) near-freezing, nighttime winter water temperatures and occasional anchor ice, (2) a prolonged period of high discharge in late spring and early summer (3) a brief summer, and (4) a prolonged period of moderate stream discharge in autumn when the substratum is stable and food is abundant.

Despite early biogeographical research on aquatic insects of the Sierra Nevada in California (see Usinger 1956), phenological data and information on structure of benthic insect communities in streams of this range are very limited. There is a similar lack of information on production of stream fauna and on the species composition and seasonality of stream periphyton. We report results of a four-year investigation of Convict Creek, a permanent snowmelt- and spring-fed stream draining a 41 km^2 watershed on the steep eastern escarpment of the Sierra Nevada. The study area includes both mesic and xeric terrestrial vegetation (Orr 1981). Objectives of this study were to determine (1) the species composition of periphyton and benthic insect communities of Convict Creek, (2) the temporal variation in population densities of common taxa, (3) basic life histories and annual production of the common benthic insects, and (4) effects of hydrologic extremes on community structure. The ecology of Convict Creek is compared to that of other streams at comparable altitudes in mountain ranges bordering the Great Basin of the western United States.

STUDY AREA

Convict Creek (Lat. 37° 37′ N, Long. 118° 50′ W) is in the Inyo National Forest in Mono County, California. The study area lies within Convict Creek basin at an altitude of 2,185 m in the reserve of the Sierra Nevada Aquatic Research Laboratory. The geology of the upper part of the basin is unusual for the Sierra Nevada in that metamorphic rather than granitic rocks predominate. The lower part of the basin, including the study area, is composed of alluvium and morainal materials from erosion and glaciation of the area above. The metamorphic rock is of two major types, siliceous hornfels and siliceous calc-hornfels (Rinehart and Ross 1964). The granitic rock is primarily quartz monzonite and granodiorite. Sandstones in the vicinity of Convict Creek are primarily quartz sandstone and calcareous quartz sandstone. Mineralogic analyses of fine sand and silt (fraction <74 μm) in the sediments of Convict Creek indicate an abundance of feldspar, quartz, and calcite.

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A Great Basin sagebrush community dominated by big sagebrush, *Artemisia tridentata* Nutt., rabbit brush, *Chrysothamnus nauseosus* (Pall.) Britt., and antelope bitterbrush, *Purshia tridentata* (Pursh) DC., covers much of the study area (Orr 1981). High desert riparian woodland occurs along the stream; dominant species of this community are quaking aspen, *Populus tremuloides* Michx., water birch, *Betula fontinalis* Sarg. and willows, *Salix* spp. Riparian meadow vegetation characterized by sedges, *Carex* spp., rushes, *Juncus* spp., and various grasses occur along the banks in low-lying areas of poorly drained soils.

Convict Creek is a perennial riffle-pool stream. Fluctuations in discharge are moderated by Convict Lake 4 km upstream and a bypass channel permitting diversion of flood water around the study area. The streambed is rocky, ranging primarily from coarse sand and pebbles to cobbles. The water is clear; suspended sediment concentrations are typically < 1 mg/liter. The stream is oligotrophic, with nitrate concentrations typically less than 10 μg/liter NO_3-N and ortho-phosphate concentrations not exceeding 0.2 μg/liter $PO_4^{3-}-P$ (Leland and Carter 1985). Silica concentrations range from 7.1 to 8.3 mg/liter SiO_2. The water is alkaline (pH 7.9 to 8.5) and always at or near saturation with respect to dissolved oxygen. Major ionic constituents (in mg/liter) determined during a period of base flow were: Ca^{2+}, 23; Mg^{2+}, 0.3; K^+, 0.7; Na^+, 1.4; SO_4^{2-}, 11; and Cl^-, 0.2.

The study area is the 340 m reach of Convict Creek that was used as a control section in experimental studies of Leland and Carter (1984, 1985) and Leland et al. (1986). For a map of the area, see Leland and Carter (1984).

MATERIALS AND METHODS

Water temperature and stream discharge in the study area were monitored continuously. The temperature sensor was located 5 cm below the surface of the streambed. A water stage servo-manometer with nitrogen-purge system (bubble gage—U.S. Geological Survey 1962) was used to determine discharge from 1978 through 1980. Stream discharge in 1977 was estimated from records maintained by the Los Angeles Department of Water and Power at a site approximately 2 km upstream of the study area. Degree-day estimates were calculated from 1 January.

Samples of benthic algae were scraped from 5 x 5 cm delineated areas of the upper surfaces of three separate cobbles (approximately 8 to 12 cm diameter) from the middle of the stream in unshaded riffles. Six samples (three per site) were taken from the same two riffles (each approximately 3 m by 30 m) each date. Sampling was approximately monthly from June through November in 1979 and 1980. Only algae with chloroplasts and intact cell walls were included in the counts (Leland and Carter 1984). Numbers of individuals recorded for each taxon were cells for free and colonial species and filament fragments for filamentous forms (according to the methods of Greeson et al. 1977, section 7.3). Most diatoms were identified to species, whereas green and blue-green algae were identified to genus.

Sampling of aquatic insects was conducted monthly to bimonthly from late spring through autumn of the years 1977 through 1980. The same riffle (approximately 3 m by 50 m) was sampled each date. An invertebrate box sampler (Ellis-Rutter)[2] with a net of 0.35 mm mesh and sampling area of 0.1 m^2 was used. Sampling was from the middle of the stream and included both upstream and downstream areas of the riffle. Three samples were taken each sampling date to permit estimation of mean population densities. Samples were preserved in 70% ethanol and sorted in the laboratory with the aid of sugar flotation (Anderson 1959). All aquatic insects were identified to the lowest taxonomic level practical (genus or species). Observations on time of adult emergence, composition of the drift, and rearing of later instars were conducted to provide additional life history information.

Abundance data are expressed as population densities (individuals/cm^2 of benthic algae and individuals/0.1 m^2 of benthic insects).

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[2] Use of brand names is for identification only and does not constitute endorsement by the U.S. Geological Survey.

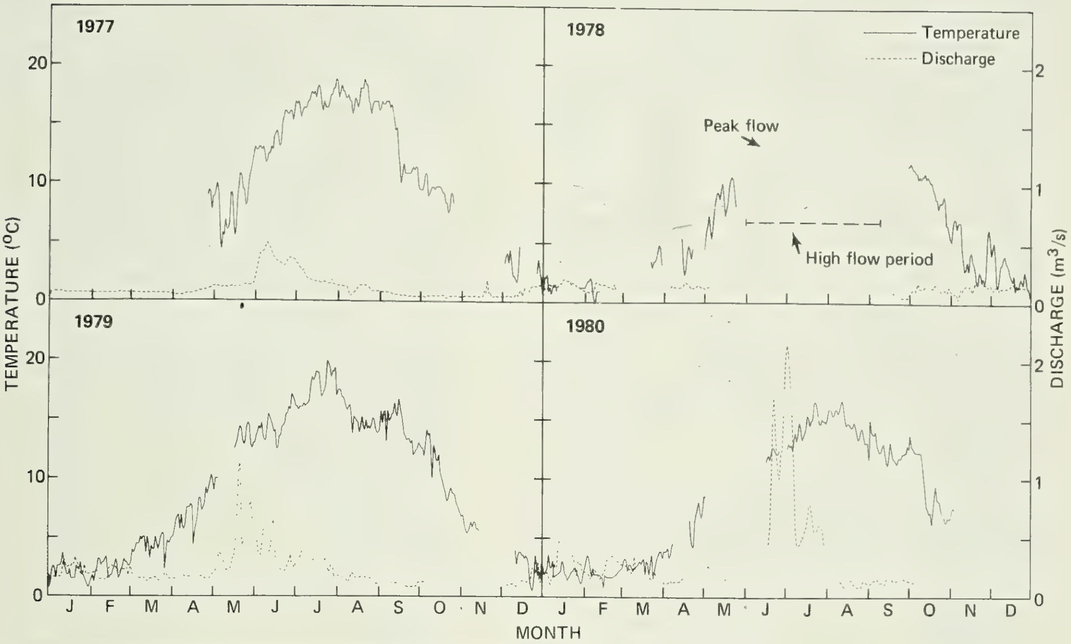

Fig. 1. Mean daily water temperature and mean daily discharge of Convict Creek.

Abundant taxa are defined as those with densities greater than about 2% of the individuals of all taxa. Common taxa are those with densities greater than 0.1% of the individuals of all taxa.

Secondary production was estimated using the size-frequency method (Hynes and Coleman 1968, Hamilton 1969, Benke 1979, Krueger and Martin 1980), with computations based on body lengths and dry weights of common taxa. Cohort production intervals, in days from hatching to the attainment of the largest aquatic size class, were determined from life history and abundance data summarized in Figure 4. Sampling began in August 1979 and continued until June 1980. Intervals between samples were 24, 38, 41, 166, and 39 days.

RESULTS AND DISCUSSION

Environmental Variables

Continuous records of stream discharge and water temperature were obtained for most of 1977 through 1980 (Fig. 1). Convict Creek is typically at or near base flow in winter (December to mid-March). The stream discharge increases in late spring due to snowmelt higher in the basin. This annual period of high discharge begins in May or June and lasts one or two months. Peak discharge (in m^3/s) was 0.50 in 1977, 1.30 in 1978, 1.15 in 1979, and 2.14 in 1980. A second high discharge period occurred in early September 1978 due to unseasonably heavy rains accompanying Hurricane Norman. Stream discharge generally declines during late summer and autumn and reaches baseflow in October.

Mean daily water temperatures in winter ranged from 0.6 to 3.6 C in 1979 and 1980 (Fig. 1). Winter air temperatures were generally lower in 1978 and 1979 than in 1977 (a mild winter) or in 1980 (when an exceptionally heavy snow cover was present). Anchor ice formed more frequently during the winters of 1978 and 1979 than during the other two years. Mean daily water temperatures during summer (July-August) were higher in 1977 and 1979 than in 1980. Daily means in October did not vary substantially among years.

Periphyton

COMMUNITY COMPOSITION.—The periphyton of Convict Creek is highly diverse (Table 1). A total of 30 genera (at least 104 species) of diatoms, 24 genera of green algae, and 29 genera of blue-green algae were identified

TABLE 1. Benthic algae of Convict Creek

CHLOROPHYTA
Ankistrodesmus falcatus (Corda) Ralfs
Carteria spp.
Chaetophora spp.
Characium spp.
Cladophora spp.
Closterium spp.
Coelastrum spp.
Coleochaete spp.
Cylindrocapsa spp.
Dictyosphaerium spp.
Draparnaldia spp.
Elakatothrix spp.
Gloeocystis spp.
Mougeotia spp.
Oedogonium spp.
Oocystis spp.
Pediastrum spp.
Protoderma spp.
Rhizoclonium spp.
Spirogyra grantiana Transeau
Stigeoclonium spp.
Ulothrix spp.
Zygnema spp.

EUGLENOPHYTA
Euglena spp.
Trachelomonas spp.

PYRROPHYTA
Ceratium hirundinella (O.F. Mull) Dujardin

CHRYSOPHYTA
Xanthophyceae
Vaucheria spp.

Chrysophyceae
Dinobryon cylindricum Imhof *ex* Ahlstrom
D. sertularia Ehr.

Bacillariophyceae
Achnanthes bergiani Cleve-Euler
A. exigua Grun.
A. lanceolata Breb. *ex* Kutz.
A. linearis (W. Sm.) Grun.
A. minutissima Kutz.
Amphora ovalis (Kutz.) Kutz.
A. perpusilla (Grun.) Grun.
Amphipleura pellucida Kutz.
Asterionella formosa Hass.
Ceratoneis (=Hannaea) *arcus* Ehr. Kutz.
Cocconeis pediculus Ehr.
C. placentula euglypta (Ehr.) Cl.
C. placentula lineata (Ehr.) V.H.
Cyclotella comta (Ehr.) Kutz.
C. kutzingiana Thwaites
C. stelligera Cl. and Grun.
Cymbella affinis Kutz.
C. brehmii Hust.
C. lanceolata (Ag.) Ag.
C. mexicana (Ehr.) Cl.
C. microcephala Grun.
C. minuta minuta Hilse *ex* Rabh.
C. perpusilla Cl.
C. prostrata (Berk.) Cl.
C. sinuata Greg.
C. tumida (Breb *ex* Kutz.) V.H.

Table 1 continued.

Denticula spp.
Diatoma hiemale (Lyngb.) Heib.
D. vulgare Bory
Diploneis ovalis oblongella (Naeg.) Cl.
Epithemia adnata adnata (Kutz.) Breb.
E. sorex Kutz.
E. turgida (Ehr.) Kutz.
E. turgida granulata (Ehr.) Brun
Fragilaria brevistriata inflata (Pant.) Hust.
F. construens (Ehr.) Grun.
F. construens binodis (Ehr.) Grun.
F. crotonensis Kitton
F. leptostauron (Ehr.) Hust.
F. pinnata Ehr.
Frustulia spp.
Gomphoneis herculeana (Ehr.) Cl.
Gomphonema acuminatum Ehr.
G. dichotomum Kutz.
G. olivaceum (Lyngb.) Kutz.
G. parvulum (Kutz.)
G. subclavatum (Grun.) Grun.
G. truncatum Ehr.
Hantzschia spp.
Melosira varians Ag.
Navicula arvensis Hust.
N. aurora Sov.
N. bacillum Ehr.
N. capitata Ehr.
N. cocconeiformis Greg. *ex* Grev.
N. cryptocephala Kutz.
N. hambergii Hust.
N. lanceolata (Ag.) Kutz.
N. pupula Kutz.
N. radiosa Kutz.
N. rhynchocephala Kutz.
N. salinarum Grun.
N. seminulum Grun.
N. tripunctata (O.F. Mull.) Bory
Neidium spp.
Nitzschia acicularis W. Sm.
N. actinastroides (Lemm) v. Goor
N. amphibia Grun.
N. dissipata (Kutz.) Grun.
N. frustulum (Kutz.) Grun.
N. linearis W. Sm.
N. palea (Kutz.) W. Sm.
N. sigma (Kutz.) W. Sm.
N. vitrea Norman
Pinnularia nodosa (Ehr.) W. Sm.
P. rupestris Hantz.
Rhopalodia gibba (Ehr.) O. Mull.
Stauroneis spp.
Stephanodiscus spp.
Surirella spp.
Synedra acus Kutz.
S. radians Kutz.
S. rumpens Kutz.
S. rumpens fragilaroides Grun.
S. ulna (Nitz.) Ehr.
S. ulna oxyrhynchus Kutz.
S. ulna spathulifera (Grun.) V.H.
Tabellaria fenestrata (Lyngb.) Kutz.

RHODOPHYTA
Batrachospermum spp.

Table 1 continued.

CYANOPHYTA
- *Amphithrix* spp.
- *Anabaena* spp.
- *Anabaenopsis* spp.
- *Aphanocapsa* spp.
- *Calothrix* spp.
- *Chamaesiphon incrustans* (Grun.)
- *Chroococcus* spp.
- *Coelosphaerium* spp.
- *Colosterium* spp.
- *Cylindrospermum* spp.
- *Dactylococcopsis* spp.
- *Dichothrix* spp.
- *Gloeotrichia* spp.
- *Hapalosiphon* spp.
- *Lyngbya* spp.
- *Merismopedia* spp.
- *Microcystis* spp.
- *Nodularia* spp.
- *Nostoc* spp.
- *Oscillatoria* spp.
- *Phormidium* spp.
- *Plectonema* spp.
- *Raphidiopsis* spp.
- *Rivularia* spp.
- *Schizothrix* spp.
- *Scytonema* spp.
- *Spirulina* spp.
- *Stigonema* spp.
- *Tolypothrix* spp.

during the study. All of the most abundant taxa are diatoms, except for a few blue-greens that attain high abundance in late spring–summer. The composition of benthic algae in Sierra Nevada streams is poorly known. Hoffman (1978) provided a partial inventory (23 species) of diatoms in Martis Creek, a perennial stream in the Truckee River Basin. Twelve of the 23 species, all cosmopolitan in their distribution, are common in both Martis Creek and Convict Creek. Sanford (1972) listed the conspicuous benthic algae in streams draining Feeley Lake and Round Lake in Tahoe National Forest; the dominant taxa in these streams are not abundant in Convict Creek.

SEASONAL ABUNDANCES OF COMMON TAXA.—Mean population densities of 22 common benthic algae in Convict Creek from late spring through autumn are presented in Figure 2. An ordination method (detrended correspondence analysis [Hill 1979, Hill and Gauch 1980, Leland and Carter 1986]) was used to objectively order the taxa. The ordering emphasizes the seasonal progression from taxa most abundant in spring to taxa most abundant in autumn. The major exceptions were *Fragilaria crotonensis*, characteristically a planktonic species and perhaps an opportunist in the periphyton of Convict Creek (Convict Lake is 4 km upstream), and *Fragilaria construens*. Both taxa were highly variable spatially.

Late spring–summer: The principal species of *Gomphonema* (*parvulum*, *subclavatum*, and *truncatum*) in Convict Creek were apparently most abundant in winter and early spring. The dominant algae in late spring and summer were the diatom *Achnanthes minutissima* and the blue-green *Lyngbya* spp.; population densities of the two co-dominants declined markedly by early autumn. Densities of *A. minutissima* and *Lyngbya* spp. were 3 and 11 times higher, respectively, in late spring 1980 than in late spring 1979, which accounted for a higher standing stock (total number of individuals of all taxa) in 1980. Other diatoms that had population maxima in late spring-summer are *Synedra acus*, *S. rumpens*, and *S. ulna*. These species are early colonizers of denuded surfaces in Convict Creek (Leland and Carter 1984). The highly invasive blue-green *Chamaesiphon incrustans* was also most abundant in late spring-summer.

Late summer–early autumn: Stream discharge was substantially higher in late spring–summer 1980 than during the same period in 1979. By early August between-year differences in periphyton assemblages were apparent. The blue-green *Oscillatoria* spp. was very abundant in the summer of 1979 but not in 1980. The lower population density of *Oscillatoria* spp. in summer 1980 may have been related to the higher stream discharge. However, the rate of primary production was lower in 1980 (Leland and Carter 1985). Primary production (estimated from three-week accumulations of autotrophic biomass on artificial substrates) ranged from 0.22 to 0.58 mg C/m^2/hr in summer-autumn 1979, but it declined to 0.08 to 0.28 mg C/m^2/hr after peak discharge in summer 1980, apparently due to phosphorus-limited growth. *Oscillatoria* species are generally abundant only in areas of nutrient enrichment (VanLandingham 1982). The decrease in density of this taxon in summer 1980 may have been attributable to slower growth in a phosphorus-deficient environment.

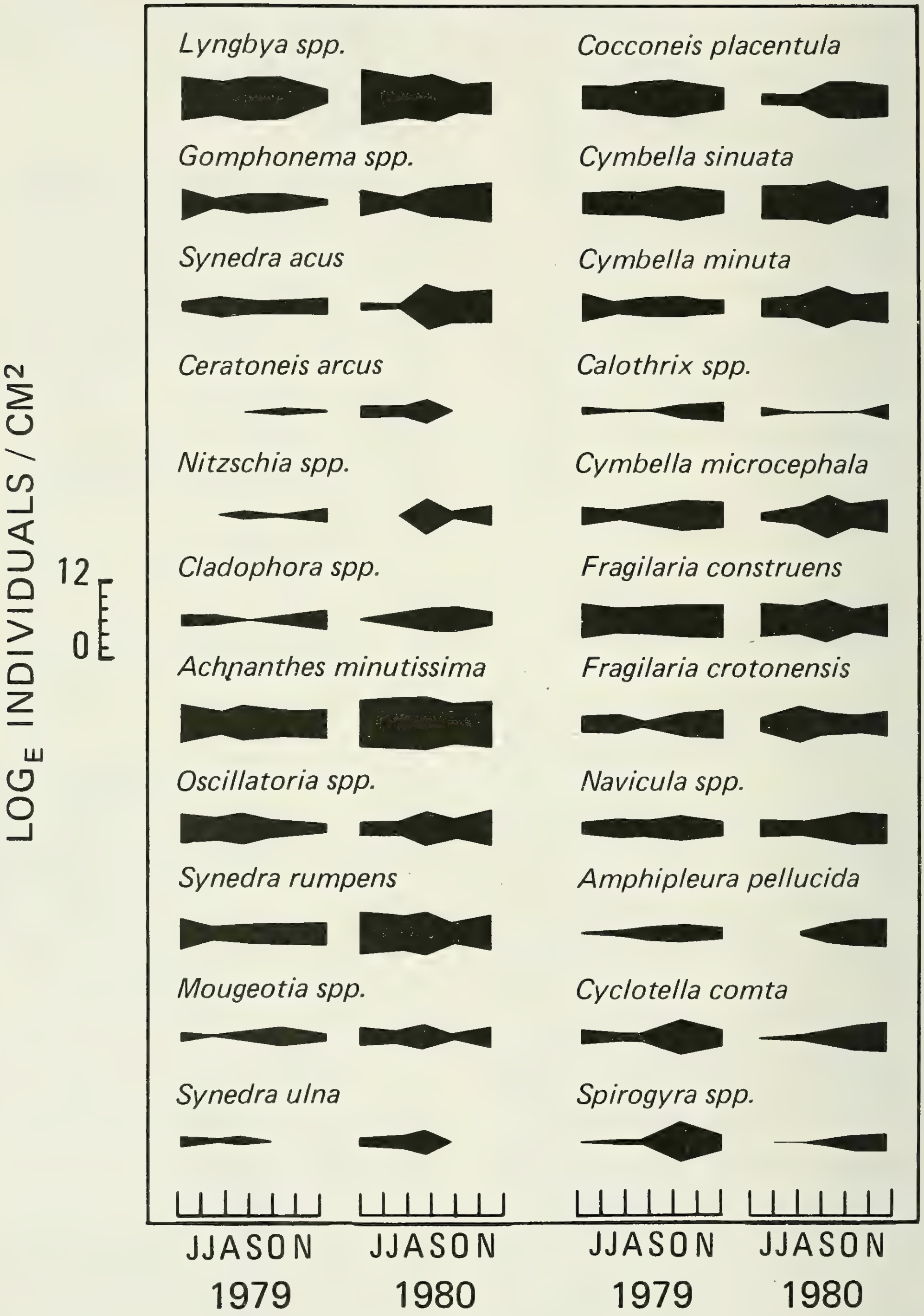

Fig. 2. Mean population densities (n = 6) of common benthic algae on streambed cobble of Convict Creek. Densities were normalized by natural logarithmic transformation prior to calculating means and standard errors. Seasonal population trends identified in the text are based on mean densities differing by at least the sum of the standard errors of the means.

TABLE 2. Benthic insects of Convict Creek.

EPHEMEROPTERA
Siphlonuridae
+ *Ameletus* sp.

Baetidae
Baetis devinctus Traver
Baetis tricaudatus Dodds
+ *Baetis* spp.
+ *Callibaetis pacificus* Seeman

Heptageniidae
Cinygmula sp.
+ *Epeorus dulciana* (McDunnough)
* *Epeorus longimanus* (Eaton)
Ironodes lepidus Traver
Rhithrogena sp.

Ephemerellidae
* *Caudatella heterocaudata* (McDunnough)
* *Caudatella hystrix* (Traver)
Drunella doddsi (Needham)
* *Drunella flavilinea* (McDunnough)
Drunella grandis (Eaton)
* *Drunella pelosa* (Mayo)
* *Ephemerella infrequens* McDunnough
Serratella tibialis (McDunnough)

Tricorythidae
Tricorythodes minutus Traver

Leptophlebiidae
* *Paraleptophlebia pallipes* (Hagen)

PLECOPTERA
Pteronarcidae
* *Pteronarcys princeps* Banks
* *Pteronarcella regularis* Hagen

Peltoperlidae
Yoraperla brevis (Banks)

Nemouridae
Malenka sp., probably *californica* (Claassen)
* *Zapada cinctipes* (Banks)

Perlidae
* *Calineuria californica* (Banks)
Doroneuria baumanni Stark & Gaufin
* *Hesperoperla pacifica* (Banks)

Chloroperlidae
* *Sweltsa* sp., probably *pacifica* (Banks)

HEMIPTERA
Belostomatidae
Belostoma bakeri Montd.

Corixidae
Corisella inscripta Uhler
Sigara washingtonensis Hungerford

MEGALOPTERA
Corydalidae
Orohermes crepusculus (Chandler)

TRICHOPTERA
Philopotamidae
* *Wormaldia* sp., probably *gabriella* Banks

Polycentropodidae
+ *Polycentropus* sp.

Hydropsychidae
* *Arctopsyche grandis* (Banks)

Table 2 continued.

* *Hydropsyche oslari* (Banks)

Rhyacophilidae
* *Rhyacophila acropedes* Banks
Rhyacophila angelita Banks
* *Rhyacophila vaccua* Milne
+ *Rhyacophila* sp.

Glossosomatidae
Agapetus taho Ross
* *Glossosoma califica* Denning

Hydroptilidae
+ *Agraylea saltesa* Ross
+ *Hydroptila* spp.
+ *Oxyethira* sp.

Brachycentridae
* *Brachycentrus americanus* (Banks)
+ *Micrasema* sp.

Lepidostomatidae
* *Lepidostoma cascadense* (Milne)
* *Lepidostoma rayneri* Ross
+ *Lepidostoma* sp.

Limnephilidae
+ *Dicosmoecus atripes* (Hagen)
+ *Neophylax* sp.

Leptoceridae
Triaenodes sp.

LEPIDOPTERA
Pyralidae
undetermined genus

COLEOPTERA
Dytiscidae
Agabus obsoletus (LeConte)
Bidessus sp.
Deronectes striatellus (LeConte)
Deronectes sp.
Hydroporus sp.
Laccophilus decipiens LeConte
Rhantus binotatus Harris

Hydrophilidae
Ametor scabrosus (Horn)
Berosus sp.
Laccobius ellipticus LeConte
undetermined genus

Hydraenidae
Hydraena vandykei d'Orchymont
Ochthebius interruptus LeConte

Elmidae
Cleptelmis addenda (Fall)
+ *Lara avara* LeConte
Narpus sp.
Optioservus divergens (LeConte)
Optioservus quadrimaculatus (Horn)
Zaitzevia parvula Horn

DIPTERA
Deuterophlebiidae
* *Deuterophlebia nielsoni* Kennedy

Blephariceridae
Agathon comstocki Kellogg

Tipulidae
* *Antocha monticola* Alexander

Table 2 continued.

	Cryptolabis sp.
+	*Dicranota* sp.
	Gonomyia sp.
+	*Hexatoma* sp.
	Pedicia sp.
	Tipula spp.
+	**Psychodidae**
	Pericoma sp.
	Maruina sp.
+	**Ceratopogonidae**
	Palpomyia or *Bezzia* spp.
	Simuliidae
*	*Simulium aureum* Fries
*	*Simulium arcticum* Malloch
+	*Simulium* spp.
	Prosimulium dicum Dyar & Shannon
	Chironomidae
	Tanypodinae
	Tanypus sp.
	Thienemannimyia group
	Diamesinae
+	*Diamesa* sp.
	Diamesa latitarsus (Goetghebuer)
	Pagastia sp.
	Prodiamesa sp.
	Orthocladiinae
	Chaetocladius spp.
	Corynoneura spp.
+	*Cricotopus* spp.
	Cricotopus bicinctus group
+	*Eukiefferiella* spp.
	Eukiefferiella bavarica group
	Eukiefferiella brevicalcar group
	Eukiefferiella potthasti group
	Krenosmittia sp.
	Nanocladius sp.
	Orthocladius spp.
	Orthocladius (*Euorthocladius*) sp.
	Pseudorthocladius sp.
	Thienemanniella sp. 1
	Thienemanniella spp.
	Chironominae
	Dicrotendipes sp.
	Polypedilum laetum (Meigen)
	Polypedilum (*Tripodura*) sp.
	Polypedilum spp.
	Pseudochironomus sp.
	Empididae
	Chelifera sp.
+	*Wiedemannia* sp.
	undetermined genus
	Muscidae
	Limnophora sp.

* Species reported by Kennedy (1967)
+Genus or family reported by Kennedy (1967)

Common diatoms in Convict Creek with population maxima during late summer–early autumn were *Cocconeis placentula lineata*, *Cymbella microcephala*, *Cymbella sinuata*, *Nitzschia frustulum*, and *N. palea*. The green algae *Mougeotia* spp. and *Cladophora* spp. were also abundant at this time. *Cymbella microcephala* and *C. sinuata* were early colonizers in late summer, whereas the other taxa were later successional species.

Autumn: Common taxa with population maxima in autumn were the diatoms *Cyclotella comta*, *Navicula* spp. (principally *cryptocephala*, *rhynchocephala* and *arvensis*), and *Amphipleura pellucida*, the green alga *Spirogyra* spp. (principally *grantiana*), and the blue-green *Calothrix* spp. By mid-October 1979 *Spirogyra* spp. was a co-dominant but in 1980 it was never very abundant, whereas *Lyngbya* spp., *Achnanthes minutissima, Cocconeis placentula lineata, Cymbella microcephala, C. sinuata, Fragilaria construens, Navicula* spp. and *Synedra rumpens* were abundant both years. By mid-November *A. minutissima, F. construens,* and *F. crotonensis* were the most abundant diatoms. *Calothrix* spp. was abundant in late autumn 1979 but not in 1980. *Spirogyra* spp. was the principal green alga in late autumn 1979, whereas *Cladophora* spp. was more abundant in 1980.

Benthic Insects

COMMUNITY COMPOSITION.—Comprehensive lists of benthic insects exist for several streams of the eastern Sierra Nevada at approximately the same altitude as Convict Creek. Three streams in the Truckee River Basin, Sagehen Creek (Gard 1961, Siegfried and Knight 1975), Berry Creek (Siegfried and Knight 1975), and Prosser Creek (Needham and Usinger 1956), have faunal compositions (comparing genera) similar to that of Convict Creek (Convict Creek taxa are listed in Table 2). However, the Truckee River Basin streams have higher densities of the ephemeropterans *Cinygmula* and *Rhithrogena*, their species of Ephemerellidae are mostly different, and we did not collect the plecopteran families Leuctridae, Capniidae, and Perlodidae (but Kennedy [1967] did report Leuctridae and Capniidae in Convict Creek). Maciolek and Tunzi (1968) listed the fauna of Laurel Creek, which is near Convict Creek but at a higher elevation. Fewer taxa are present in Laurel Creek, but benthic insect compositions of the two streams are similar.

Kennedy (1967) listed the benthic insects of

Convict Creek during 1961–1963 but presented little information on population densities; most of the common taxa we observed in 1977–1980 were also found by Kennedy (Table 2). Some apparent differences in the stream fauna between the early 1960s and late 1970s are due to difficulties in identifying immature stages and differences in sampling method. Kennedy (1967) collected extensively only from riffles, whereas midriffle benthos and drift were sampled in the present study. Notable differences between our species list and that of Kennedy (1967) are (1) that *Optioservus divergens, Ironodes lepidus, Doroneuria baumanni,* and *Malenka* (*californica*?) are common taxa now but were not reported in 1961–1963 and (2) that Kennedy (1967) found three winter stoneflies (Leuctridae and Capniidae) not observed in 1977–1980. These stoneflies typically develop in winter-spring and may have been missed in our sampling program.

SEASONALITY AND LIFE HISTORIES OF COMMON TAXA.—Mean population densities of 28 common benthic insects in Convict Creek are given in Fig. 3. The taxa are ordered by their location on the primary axis in ordination space (detrended correspondence analysis—see Leland et al. 1986). Seasonality of taxa is emphasized in the ordering. Data on population densities (which emphasize early and middle instars) are supplemented with observations on the occurrences of late instars, pupae, and adults and on length-frequency data to determine life histories (Fig. 4).

Late spring (400 to 1,200 degree-days): Taxa most abundant during May and June are considered late-spring fauna. Species in this assemblage include ephemeropterans (*Epeorus longimanus, Drunella flavilinea*, and *Caudatella heterocaudata*), plecopterans (*Calineuria californica, Doroneuria baumanni*, and *Pteronarcys princeps*), and dipterans (*Cryptolabis* sp. and *Palpomyia* spp.). The three ephemeropterans occur as middle to late instars in late spring. Their major period of growth and development is early to late spring, and adults appear during late spring and summer (Fig. 4). Nymphs are not common in autumn, so most early instars must first appear during winter (as early as December for *D. flavilinea*) or early spring. *Caudatella heterocaudata* develops somewhat later than the other two species, and most individuals emerge later in the summer. Slow growth or a diapause in autumn and early winter for eggs and early instars, followed by a rapid development in spring, is suggested for all three species. This corresponds to the "fast seasonal" type of life history described by Hynes (1970). Similar life histories have been reported for *D. flavilinea* in Idaho (Andrews and Minshall 1979) and *E. longimanus* in Alberta (Hartland-Row 1964).

Early instars of the plecopterans *C. californica, D. baumanni,* and *P. princeps* are most abundant in late spring. These species typically have a two- or three-year life cycle, and egg development requires as long as 8 to 10 months (Siegfried and Knight 1977, Barton 1980). Hatching of *C. californica* and *D. baumanni* extends over several months since early instars are also present in autumn. Rates of development of all three species are probably highest during late spring and summer (Heiman and Knight 1975, Siegfried and Knight 1977).

Cryptolabis sp. is the most abundant tipulid in Convict Creek and is especially prevalent in late spring. Development occurs primarily between August and May and individuals overwinter as middle to late instars; pupation occurs in July. The relative scarcity of early instars indicates that at this stage *Cryptolabis* sp. may be hyporheic or inhabit regions of slower current. Two other common dipterans, *Deuterophlebia nielsoni* and *Palpomyia* spp., are most abundant during late spring, but their population densities are never high. *Deuterophlebia nielsoni* is multivoltine (Kennedy 1967); however, we did not observe larvae of this species after September.

Summer (1,200 to 2,200 degree-days): Population densities of many common taxa in Convict Creek are lowest in early summer. This is generally true for temperate streams (Hynes 1970) and is due at least in part to the lag between spring adult emergence and hatch of the next generation. Nighttime air temperatures generally remain above freezing during late spring and early summer, and emergence of most species occurs at this time (see Fig. 4). Scouring of the streambed during periods of high discharge in late spring–summer also appears to contribute to population declines. Other authors (Gaufin 1959, Canton and Ward 1978, Minshall 1981) have

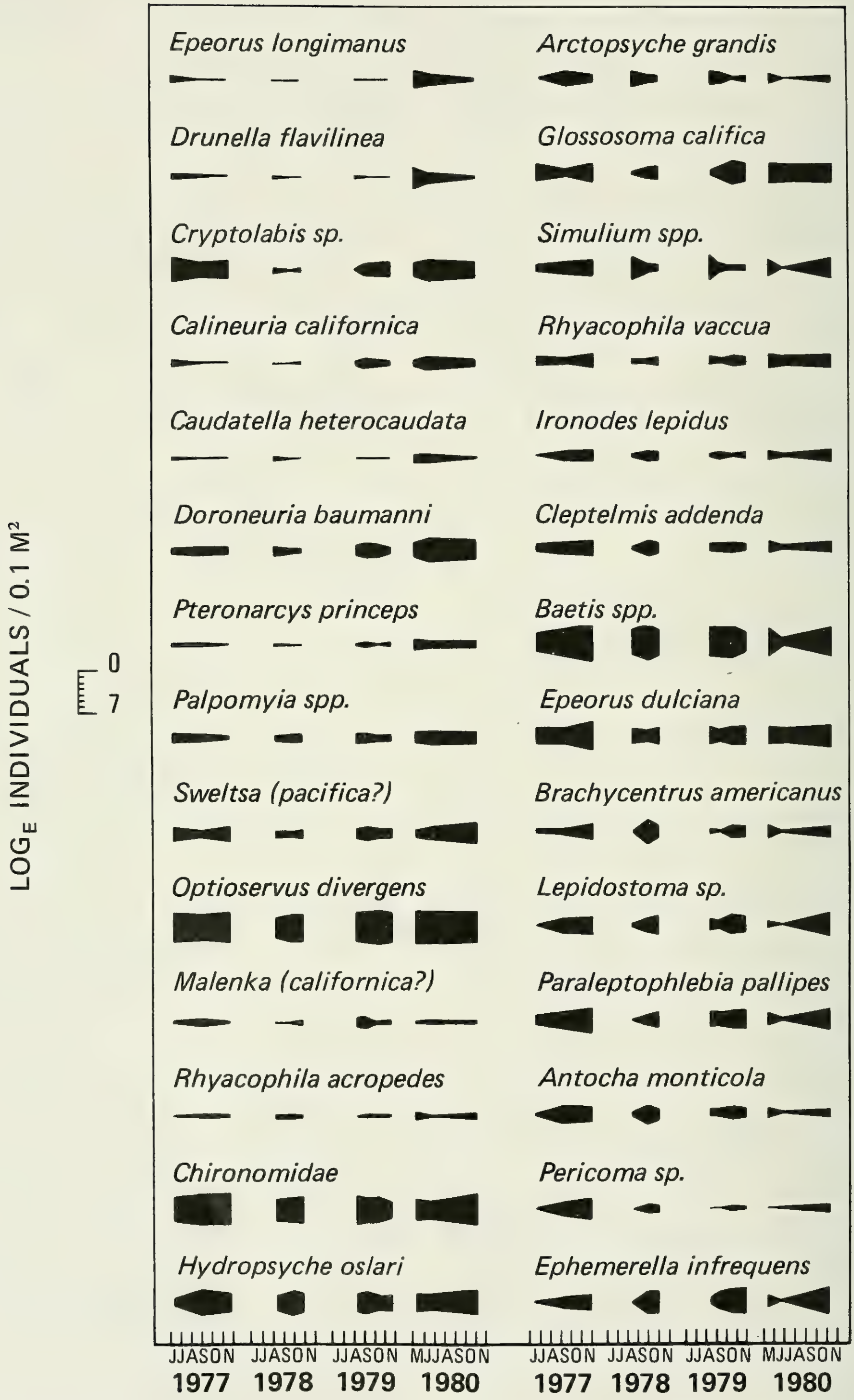

Fig. 3. Mean population densities (n = 3) of common benthic insects in riffle areas of Convict Creek. Densities were normalized by natural logarithmic transformation prior to calculating means and standard errors. Seasonal population trends identified in the text are based on mean densities differing by at least the sum of the standard errors of the means.

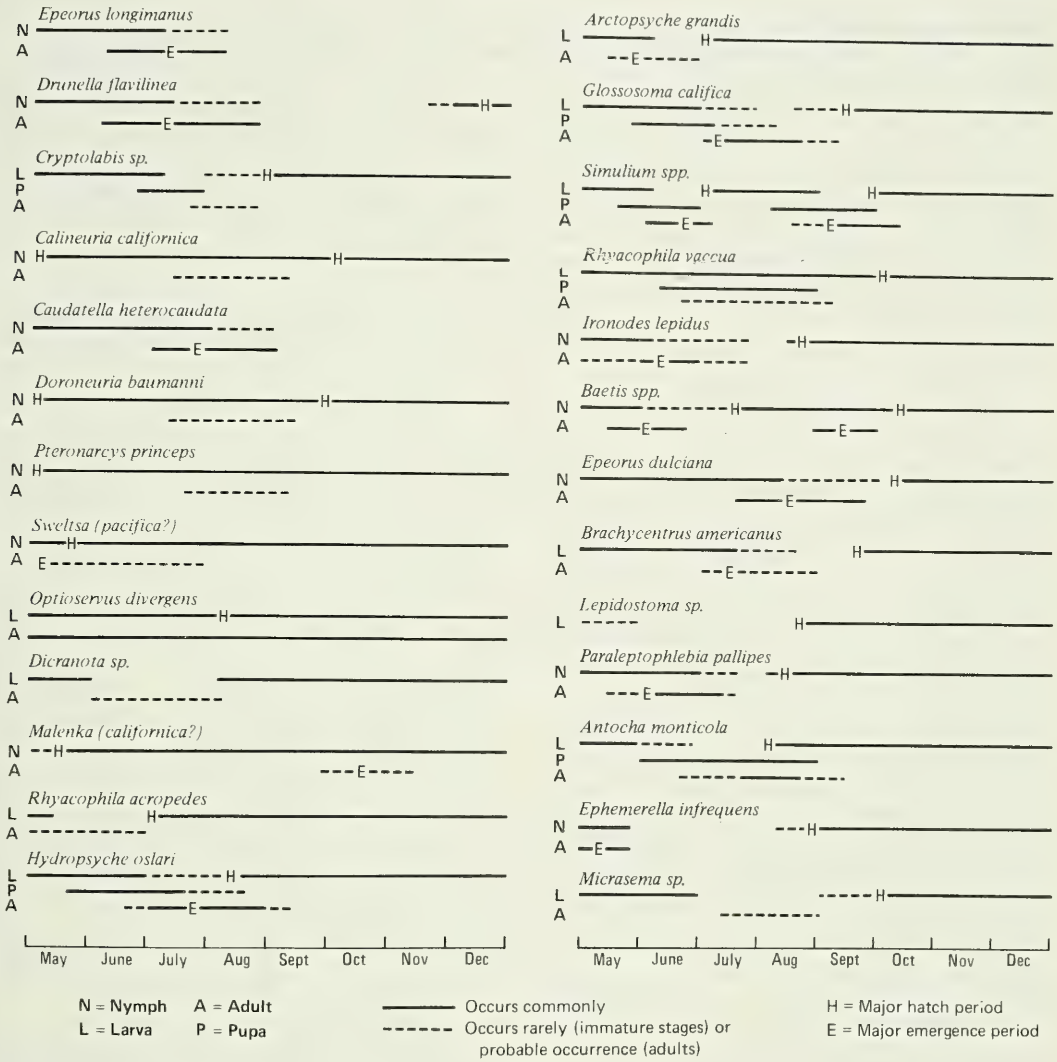

Fig. 4. Generalized life histories for common benthic insects of Convict Creek.

attributed low summer populations in streams of the western United States to the same factors.

The plecopteran *Malenka* (*californica*?) completes most of its development during summer and autumn. The main cohort emerges in October, but some individuals overwinter as late instars. The trichopteran *Arctopsyche grandis* is a common summer species; it is also the largest caddisfly in riffles and is thus an important component of the summer biomass. *Arctopsyche grandis* develops mostly between July and early September. A rapid summer development has also been reported in Idaho (Cuffney and Minshall 1981) and coastal California (Furnish 1979). The uniform size of individuals on each sampling date in Convict Creek suggests a univoltine life cycle; however, Smith (1968) found the species to be semivoltine in Idaho. *Hydropsyche oslari* is also most abundant (as early instars) in late summer, but most growth occurs after that of *A. grandis*. Growth of *H. oslari* begins about September and continues through autumn. *Rhyacophila acropedes* is another abundant summer trichopteran.

Several bivoltine and multivoltine taxa have summer cohorts. At least two species of the ephemeropteran genus *Baetis* develop between June and September. The dipterans

Simulium spp. and Chironomidae are usually most abundant from August through November. These taxa include a large number of species (see Table 2 for a list of the Chironomidae and Kennedy 1967 for a list of *Simulium* species.) Because of our inability to identify early instars, these taxa were enumerated by family; therefore, life histories cannot be described. The family Simuliidae was represented only by *Simulium* spp. in riffle samples, but a few adult *Prosimulium dicum* appeared in drift samples. A major emergence of *Simulium* spp. occurred in September 1980, but emergence was not as synchronous in other years.

Autumn (2,200 to 3,100 degree-days): Peak densities of many common taxa in Convict Creek occur in autumn. The community consists largely of early instars of "slow seasonal" species (Hynes 1970), insects that hatch quickly, develop partially during autumn, and emerge in spring (Fig. 4). Although some taxa are probably detritivores (for example, *Paraleptophlebia pallipes* and *Lepidostoma* spp.) and may have life histories timed to periods of leaf fall (Anderson and Cummins 1979), most are generalists and relative amounts of detritus and algae ingested vary seasonally (Chapman and Demory 1963, Gray and Ward 1979). Food quality probably influences life history patterns, but a more significant factor in Convict Creek may be that autumn is a period when the stream is typically at or near base flow. The moderate stream velocities may enhance survival of early instars by providing suitable substratum.

Ephemerella infrequens and *Epeorus dulciana* are common ephemeropterans in Convict Creek with autumn and early spring development. *Ephemerella infrequens* has a similar life history in Colorado (Ward and Berner 1980). *Ironodes lepidus* is less abundant in Convict Creek, but our limited data indicate a similar life history. *Paraleptophlebia pallipes* grows most rapidly in autumn, but hatching is apparently delayed in some individuals since recruitment continues through autumn. Low numbers of these taxa in June indicate a spring emergence.

Hydropsyche oslari is the dominant trichopteran by late autumn. Most individuals overwinter as third to fifth instars. This species overwinters at an earlier stage (first and second instars) in Montana (Hauer and Stanford 1982). Many other trichopterans also have peak abundances in autumn. Early instars of *Lepidostoma* spp. are common in riffles in autumn, but the taxon is rarely found there in spring. Larvae apparently move into areas of slower current in later developmental stages. *Glossosoma califica* and *Micrasema* sp. develop slowly during autumn, overwinter as early to middle instars, and pupate in late spring-summer. *Brachycentrus americanus* and *Neophylax* sp. develop to middle instars by December, but emergence does not occur until late spring or summer. *Rhyacophila vaccua* hatches during summer and autumn, overwinters primarily as middle instars, and emerges in early summer.

Chironomidae are abundant throughout autumn. Two other dipterans, *Antocha monticola* and *Pericoma* sp., also are at their maximum densities in autumn but neither is ever abundant. *Antocha monticola* completes most of its development in late summer and autumn. Although larvae were uncommon in riffles in summer, a large number of adults in August 1980 emergence samples indicates that emergence occurs throughout the summer.

Late winter/early spring (0 to 400 degree-days): Samples of benthic insects were not taken from January through April. This is apparently an active period for many species. Many late spring species must develop rapidly after overwintering as eggs or early instars. The autumn taxa are present primarily as later instars, and many of these emerge in the spring.

"Aseasonal" taxa: Some taxa are abundant throughout the snow-free months of the year, and population densities do not show strong seasonal trends. *Baetis* spp. (principally *B. devinctus* and *B. tricaudatus*) is the most abundant ephemeropteran taxon most of the year. Both species are bivoltine, with emergences in May-June and September. The autumn cohort is larger. Approximately 1,400 degree-days accumulate during development of a generation. The elmid *Optioservus divergens* appears to have a two-year life cycle (as was also described for *O. ampliatus* in eastern Canada by Le Sage and Harper 1976). Peak numbers of early instars occur between August and October, and most of this cohort reaches middle-instar stages by December.

Plecopterans in Convict Creek show less seasonal variation in abundance than do other

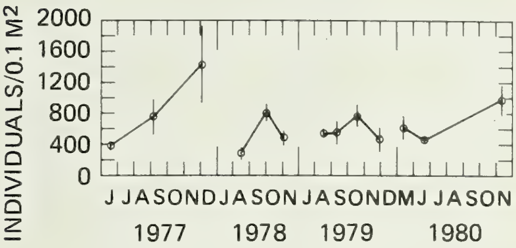

Fig. 5. Total densities (n = 3) of benthic insects in riffle areas of Convict Creek. Densities were normalized by natural logarithmic transformation prior to calculating means and standard errors.

orders of benthic insects. *Calineuria california, Doroneuria baumanni*, and *Pteronarcys princeps* all are semivoltine. However, the population density of *Sweltsa* sp., which is probably univoltine, did not vary much either. This may be due to the presence of more than one species.

YEARLY VARIATION IN RELATIVE ABUNDANCES OF TAXA.—Population densities of many common benthic insects in Convict Creek varied substantially among years. Because our sampling interval was wide and seasonal changes in population density were pronounced, only major among-year differences can be defined with certainty.

The total number of individuals of all benthic insect taxa was unusually high in late autumn 1977 (Fig. 5), a year of low discharge during all seasons and relatively high summer water temperatures (Fig. 1). Population densities of *Baetis* spp., *Paraleptophlebia pallipes, Epeorus dulciana*, and *Antocha monticola*, which hatch in autumn, were highest in late autumn 1977. Reproduction and survival of early instars of these taxa were apparently favored by the relatively mild hydrologic and climatic conditions. Except for *P. pallipes*, these taxa are all clinging, epilithic grazers (Merritt and Cummins 1984) and thus benefit from nondisruptive stream flows. *Pericoma* sp., which typically resides in fine sediments or algal mats (Usinger 1956, Merritt and Cummins 1984), was also common in riffles in autumn 1977. *Ephemerella infrequens*, another autumn-hatching ephemeropteran, was less abundant in 1977 than other years.

Sampling of benthic insects was not initiated until August in 1978, so any effects of the severe winter conditions on winter and spring fauna could not be observed. The high discharge accompanying Hurricane Norman in early autumn 1978 probably caused the low autumn densities of *Glossosoma califica, Paraleptophlebia pallipes, Epeorus dulciana, Optioservus divergens*, and some of the larger plecopterans. The severe winter conditions of early 1978 may have contributed to the population declines of the semivoltine *O. divergens, Pteronarcys princeps*, and *Doroneuria baumanni*. Severe winters appear to result in a high mortality of benthic insects. Reimers (1957) found that populations of ephemeropterans and elmid beetles in Convict Creek are reduced more by unusually cold winters than are populations of dipterans and trichopterans.

Winter air temperatures remained low longer (through March) in 1980 than in other years, but a heavy snow cover and unusually high winter baseflow prevented much anchor ice formation. The late spring-summer period of high discharge began late and continued through early August. Summer water temperatures were generally lower than in 1977 and 1979. Several taxa, including most plecopterans, were more abundant than in other years. These included *Doroneuria baumanni, Calineuria californica, Pteronarcys princeps, Rhyacophila vaccua*, and possibly *Micrasema* sp., *Palpomyia* spp., *Malenka (californica?)*, and *Sweltsa pacifica*. The greater abundances of these taxa in autumn 1980 may be the result of a more effective sorting of streambed sediments due to the unusually high discharge in late spring-summer (DeMarch 1976). The absence of anchor ice in winter may have contributed to the increased survival rate of the 1979 cohorts of *D. baumanni, C. californica*, and *P. princeps*.

Benthic Insect Production

The total annual production of herbivorous and detritivorous benthic insects in Convict Creek riffle areas was an estimated 3.9 g/m^2 (dry weight) (Table 3). Not included in this estimate is the contribution of oligochaetes and molluscs, which is approximately 10%–20% of the mean annual standing stock. The total annual production of benthic insect predators was an estimated 1.7 g/m^2. These annual production estimates compare favorably with the values of Krueger and Waters (1983) for the Caribou River and Blackhoof River, streams in Minnesota with similar sub-

TABLE 3. Annual production, mean annual standing stock, and cohort production interval (CPI) for the more abundant benthic insects in 1979–80.

	Annual production (g/m^2 dry wt.) Estimate	95% C.I.	Mean annual standing stock (g/m^2 dry wt.)	Estimated CPI (days)
PLECOPTERA				
Calineuria californica	.021	.001– .041	.006	780
Doroneuria baumanni	.233	.073– .394	.075	780
Sweltsa (pacifica?)	.012	.003– .020	.002	300
EPHEMEROPTERA				
Drunella flavilinea	.104	.070– .139	.014	210
Ephemerella infrequens	.117	.082– .152	.018	270
Paraleptophlebia pallipes	.041	.020– .062	.007	300
Baetis spp.	.937	.721–1.152	.079	150
Epeorus dulciana	.115	.061– .168	.014	300
Epeorus longimanus	.158	.079– .237	.009	150
TRICHOPTERA				
Hydropsyche oslari	.556	.320– .792	.057	300
Arctopsyche grandis	1.417	.903–1.932	.150	300
Rhyacophila vaccua	.261	.128– .393	.034	300
Glossosoma califica	.087	.025– .149	.014	300
Brachycentrus americanus	.056	.020– .092	.008	300
COLEOPTERA				
Optioservus divergens	.128	.098– .158	.069	660
Cleptelmis addenda	.003	.001– .005	.002	660
DIPTERA				
Simulium spp.	.099	.049– .149	.007	120
Chironomidae	.12	—	.012	—

strate but higher discharge and nutrient concentrations. Annual production of herbivores/detritivores in the two streams was 4.6 g/m^2 and 6.3 g/m^2 (corrected to dry weight), respectively, and the annual production of predators was 0.94 g/m^2 and 1.1 g/m^2.

There are several potential sources of error in the production estimates. Some large insects, such as *Pteronarcys princeps* and certain tipulids, may have contributed substantially to production in Convict Creek, but these individuals were not abundant enough to estimate production with confidence. Multiple-species populations (*Baetis* spp., *Simulium* spp.) and sexual dimorphism may have yielded overestimations because the size frequency method assumes that all individuals can reach the largest size class. Although nonlinear growth has been shown not to affect production estimates severely (Hamilton 1969, Cushman et al. 1978), taxa such as *Arctopsyche grandis* are less accurately estimated. Emigration from the sampled area (riffles) during some portion of the life cycle, such as with *Paraleptophlebia pallipes* (Anderson and Lehmkuhl 1968), also would give an inaccurate estimate. Finally, the production estimates may be biased due to unequal sampling intervals.

Stream conditions during the study period (mid-August 1979 to mid-June 1980) were not extreme. There was little anchor ice during winter, and the annual high discharge in late spring–summer was delayed. Consequently, insect mortalities were probably not unusually high. With most taxa hatching during summer and autumn, the period of highest mortality (early instars) was well sampled. Exceptions were *Epeorus longimanus* and *Drunella flavilinea*, which hatch in late autumn–winter.

Phenology

This investigation was not designed as a watershed phenological study, but rather a discussion of major recurring climatic and hydrologic events that influence life history patterns in Convict Creek. Winter is a harsh season lasting approximately four months (December through mid-March), when the stream is at or near baseflow, nighttime water temperatures are near freezing, and anchor ice forms occasionally. The dominant winter periphyton are diatoms (*Achnanthes, Fragi-*

laria, and *Gomphonema*) and primary production is low. It is a period of activity for many benthic insects, with taxa that reproduce in autumn present primarily as later instars. Unusually cold winters cause a high but selective mortality of benthic insects (Reimers 1957). Despite low water temperatures, brown trout (*Salmo trutta* L.) feed throughout the season (Jenkins 1969).

The water temperature begins to rise about mid-March and increases through June or July. Snowmelt in higher areas of Convict Creek Basin causes a substantial increase in discharge, beginning in May or June, which lasts for one to two months. In early summer a dense riparian canopy dominated by willows and quaking aspen develops in some stream reaches. The high discharge in late spring–summer is accompanied by declines in standing crops of periphyton and benthic insects.

Succession in the periphyton community is interrupted by scouring of the streambed in late spring and early summer. Relative abundances of periphyton taxa in late summer and autumn appear to reflect the magnitude of discharge in late spring–summer and the availability of nutrients (see also Leland and Carter 1985). When stream discharge in late spring was exceptionally high and primary productivity relatively low, the community was dominated by early-colonizing diatoms during summer; diatoms and filamentous green and blue-green algae were all abundant in autumn. When stream discharge in late spring was only moderately high and the rate of production relatively high, blue-green algae dominated in summer and remained abundant in autumn.

There is a total emergence (hence reproductive) period of at least seven months (April–October) for benthic insects, but most species emerge in late spring and early summer. Low population densities during late spring and early summer are thus due at least in part to the lag between emergence and hatch of the next generation. Scouring of the streambed also appears to contribute to the population declines.

Summer is the only season when nighttime air temperatures consistently remain above freezing; stream discharge declines progressively during this period. Later successional species of periphyton are relatively more abundant in summer than in late spring, and primary productivity is at its annual maximum. Some bivoltine and multivoltine benthic insects have summer cohorts and grow more rapidly than do individuals of the autumn cohorts.

Autumn is a season of declining water temperature and stream discharge, and baseflow is reached in October. Leaf-fall occurs from mid-September through October, with leaf litter in the stream most abundant in October. Between-year differences in periphyton composition were large, apparently due to environmental factors influencing the relative abundances of taxa at earlier successional stages (see also Leland and Carter 1986). Most slow-seasonal and multivoltine insects hatch during autumn, so this is a period of high abundance of early instars. Some of these are detritivorous (for example *Paraleptophlebia pallipes* and *Lepidostoma* spp.) and may have life histories timed to the autumn abundance of leaf litter.

ACKNOWLEDGMENTS

The contributions of Charles B. Doherty, Thomas L. Dudley, and William H. Peeler in fieldwork and in the identification and enumeration of benthic insects are gratefully acknowledged. The identifications were confirmed whenever possible using museum specimens of the California Academy of Sciences, San Jose State University, and Oregon State University. Rearing of specimens was done in some instances to aid in the identifications. Larry J. Tilley and Suzanne F. Muzzio verified identifications of the Chironomidae. All the above individuals are or were employees of the U.S. Geological Survey at the time the work was done. Sam L. VanLandingham, consulting biologist, did early identifications of the green algae and blue-green algae. The program for computing secondary production was obtained from Charles C. Krueger (Department of Entomology, Fisheries and Wildlife, University of Minnesota). Permission to conduct studies in Convict Creek was granted by the governing board of the Sierra Nevada Aquatic Research Laboratory, University of California at Santa Barbara. Scott D. Cooper, Frank F. Hooper, Allen W. Knight, and Keith V. Slack reviewed the manuscript.

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DIATOM FLORA OF COWBOY HOT SPRING, MONO COUNTY, CALIFORNIA

Laura Ekins[1] and Samuel R. Rushforth[1]

ABSTRACT.—The diatom flora of Cowboy Hot Spring, Mono County, California, was studied. Two habitats, one at 37C and one at 41C, were examined. Fifty-six taxa were identified from our samples. These taxa were mostly broadly distributed forms, and no endemic species were encountered. The dominant taxon was *Nitzschia frustulum,* followed by *Achnanthes gibberula, Achnanthes exigua, Nitzschia hantzschiana*, and *Navicula cincta*.

Interest in natural thermal waters has increased substantially during the past few years. Early studies of these environments were generally concerned with Cyanophyta or the faunas of such habitats (Edwards 1868, Davis 1897, Tilden 1897, 1898). These authors often expressed surprise that organisms could exist in thermal environments and were interested in the upper temperature tolerance of thermophilic species.

Diatoms were not studied systematically until some time later (Lacsny 1912, Oestrup 1918, Strom 1921, Famin 1933, Springer 1930), when they were found to be common in hot springs. More extensive studies were begun in the 1940s (Negoro 1940, Emoto and Hirose 1940, Emoto and Yoneda 1941, Yoneda 1942a, 1942b) and have continued to the present time (Whitford 1956, Yoneda 1962, Thomas and Gonzalves 1965a, 1965b, 1966a-e, Biebl and Kusel-Fetzmann 1966, and others). Diatoms also have recently been studied in several western North American springs (Kaczmarska and Rushforth 1983, St. Clair and Rushforth 1977, Stockner 1967a, 1967b, 1968, Rushforth et al. 1986).

Cowboy Hot Spring of the Mono Basin thermal area of eastern California is one of many thermal springs in the Basin and Range Geological Province (Great Basin). This province occurs east of the Sierra Nevada Mountains, between the Snake River and the Mojave Desert, and extends across Nevada into western Utah.

The Great Basin is characterized by a thinning of the earth's crust, more than 200 north/south-oriented mountain ranges with associated valleys (Nelson 1981), an abundance of thermal springs, and a cold desert climate. These features appear to be a result of several geological phenomena, including the continued spreading of the American Plate through the center of the Great Basin, past subduction of the Pacific Plate under the American Plate (Miller 1983), and the uplift of the Sierra Nevada.

Thermal springs have been characterized as waters with a temperature 6–9C greater than the mean annual air temperature of the adjacent area (Tarbuck and Lutgens 1984). A more detailed classification of thermal springs is that of Elenkin (Kol 1932), where waters below 15C were termed hypothermal, between 15C and 30C as mesothermal, and above 30C as euthermal. Water temperature in thermal springs generally remains quite constant because the source water is continuously heated by tectonic events.

We have studied the diatom flora of Cowboy Hot Spring to compare the flora with that of other thermal waters of western North America. This euthermal spring is of particular interest since its temperature of 41C is near the upper temperature limit for eukaryotic organisms (Ruttner 1963). The present paper lists and illustrates all known diatom taxa in Cowboy Hot Spring.

SITE DESCRIPTION AND COLLECTIONS

Cowboy Hot Spring is at 37° 38.6′ N latitude and 118° 45.45′ W longitude in Mono County, California. A concrete tub has been built around the source water, which is 41C. A runoff stream from the source contains water at 37C 3 m from the tub. Water flow is 150 l/min, and the total dissolved solids are 150 ppm (California Geol. Map 1980).

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All sampling was done 26 August 1981. Samples were taken from both the concrete tub and the runoff stream. Composite samples were collected by scraping the sides of the concrete tub and obtaining visible algae and placing these collections into vials. Stones and submerged wood in the stream were scraped, and these scrapings, together with visible algae and small amounts of sediment, were placed into vials. Composite samples of this type were obtained to insure that as many taxa as possible would be collected, since the primary thrust of this study was a floristic survey. All samples were stored at air temperature and returned to our laboratory at Brigham Young University.

METHODS

Diatoms were cleared with nitric acid following standard methods using boiling nitric acid (St. Clair and Rushforth 1977), and strewn mounts using Naphrax high resolution mounting medium were prepared. Slides were studied using Zeiss RA microscopes with Nomarski and bright field illumination. Photographs of each taxon were obtained using Nikon AFM photomicrographic equipment.

A minimum of 500 frustules was counted on each slide to calculate the relative density for each taxon in each sample. Species diversity of each sample was measured by calculating the Shannon-Weaver index (Shannon and Weaver 1963, Margalef 1958, Patten 1962).

Permanent diatom slides are in the collections at Brigham Young University.

RESULTS AND DISCUSSION

Fifty-six diatom taxa in 20 genera were identified in samples from Cowboy Hot Spring. Most of the taxa encountered are cosmopolitan, eurythermal forms and none were endemics. Kaczmarska and Rushforth (1983) found 136 diatom taxa in Blue Lake Warm Spring, in the Great Basin, a somewhat cooler spring at 29C than Cowboy Hot Spring, which might account for much of the difference in species diversity between the two sites.

Twelve taxa in Cowboy Hot Spring had an average relative density above 1.0. *Nitzschia frustulum* (Kuetz.) Grun. was the most abundant, with an average density of 31%, followed by *Achnanthes gibberula* Grun. (10.3%), *Achnanthes exigua* Grun. (10.1%), *Nitzschia hantzschiana* Rabh. (9.3%), *Navicula cincta* Ralfs (8.6%), *Anomoeoneis sphaerophora* (Ehr.) Pftiz. (6.8%), *Nitzschia communis* Rabh. (4.1%), *Achnanthes exigua* var. 1 (3.1%), *Nitzschia valdecostata* Lange-Bert. and Simon. (2.2%), *Navicula cryptocephala* var. *veneta* (Kuetz.) Rabh. (1.6%), *Rhopalodia operculata* (C.A.Ag.) Hakan. (1.6%), and *Denticula elegans* Kuetz. (1.2%).

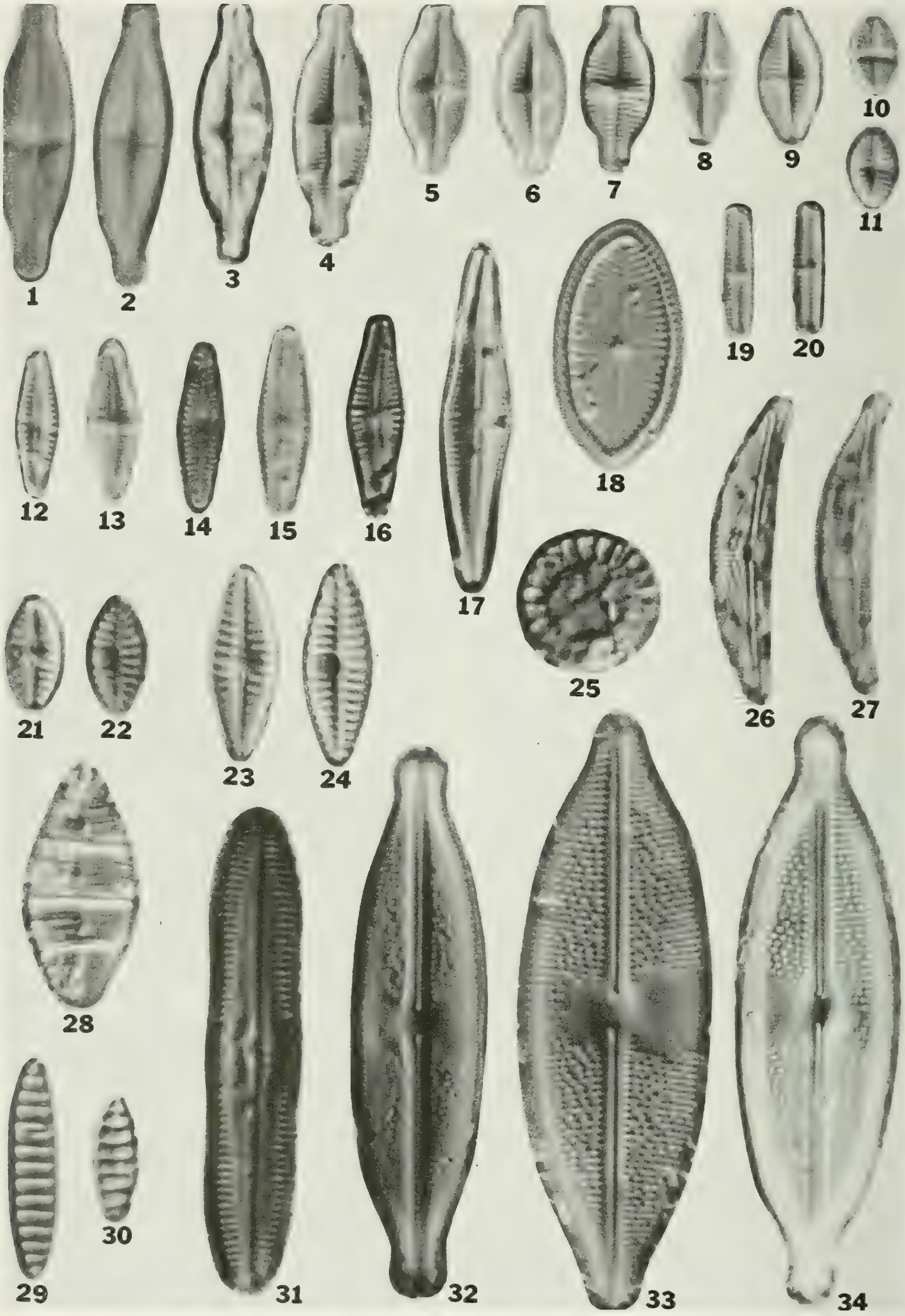
Kaczmarska and Rushforth (1983) found 17 taxa with importance values above 1.0 in Blue Lake Spring. Three of these also occurred in Cowboy Hot Spring, although none of them had average densities above 1.0%. Stockner (1967a) found 12 species common in waters above 35C in Yellowstone National Park. Eight of these taxa were also found in Cowboy Hot Spring. These included *Achnanthes gibberula* Grun., *Achnanthes lanceolata* Breb., *Amphora coffeaeformis* (Ag.) Kuetz., *Denticula elegans* Kuetz., *Gomphonema parvulum* Kuetz., *Navicula cincta* Ralfs, *Pinnularia microstauron* (Ehr.) Cl., and *Rhopalodia gibberula* (Ehr.) O.Muell.

None of the important taxa in Cowboy Hot Spring was confined to the stream or tub. However, several taxa did show a trend toward being restricted to one habitat or the other. Those reaching maximum development in the concrete tub were *Cocconeis placentula* var. *lineata* (Ehr.) V. H., *Denticula elegans* Kuetz., *Epithemia argus* (Ehr.) Kuetz., *Fragilaria construens* var. *venter* (Ehr.) Grun., and *Tabellaria quadrisepta* Knuds. Those with maximum development in the stream were *Achnanthes linearis* Grun., *Navicula confervacea* var. *peregrina* (W.Sm.) Grun., *Nitzschia microcephala* Grun., and *Pinnularia appendiculata* (Ag.) Cl. The Shannon-Weaver index value for the concrete tub was 3.67, and the stream value was 3.30.

A taxonomic section follows with a description of each taxon. A short discussion is included where appropriate.

TAXONOMIC SECTION

Achnanthes exigua Grun., Figs. 1–7. Valves 12.5–21.5 μm long by 5–6 μm wide; raphe valve striae 25–28 in 10 μm; rapheless valve striae 24–26 in 10 μm. This taxon oc-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Figs. 1–34. Diatom species: 1–7, *Achnanthes exigua*; 8–11, *Achnanthes exigua* var. 1; 12–17, *Achnanthes gibberula*; 18, *Cocconeis placentula* var. *lineata*; 19–20, *Achnanthes linearis*; 21–24, *Achnanthes lanceolata*; 25, *Cyclotella meneghiniana*; 26–27, *Amphora veneta*; 28, *Diatoma hiemale* var. *mesodon*; 29–30, *Denticula* cf. *parva*; 31, *Caloneis ventricosa* var. *truncatula*; 32–34, *Anomoeoneis sphaerophora*. All figures are 2000X.

curred at both sites but was most common in the stream, where it reached 14.0% relative density.

Achnanthes exigua var. 1, Figs. 8–11. Valves orbicular to elliptical with rounded to rostrate ends, 5–10 μm long by 3.5–5 μm wide; raphe valve with narrow, linear axial area and narrow, rectangular central area; rapheless valve with less distinct central area, often formed from one or two shortened striae; striae 22–24 in 10 μm on both valves. We considered several taxa for the placement of these specimens but were not satisfied with their fit. It seems probable that they belong with *A. exigua* except that valve shape differs somewhat and striae are slightly coarser. This taxon was present at about 3% relative density in samples from both collecting sites.

Achnanthes gibberula Grun., Figs. 12–17. Valves 5–26.5 μm long by 3–5.5 μm wide; striae 20–22 in 10 μm on both valves. Several of our specimens were shorter than ordinarily observed for this taxon. Even so, an unbroken series from very small to the largest specimens was observed. *A. gibberula* was abundant in the Cowboy Hot Tub system, with a relative density of 14.8% in the concrete tub and 5.8% relative density in the stream.

Achnanthes lanceolata Breb., Figs. 21–24. Valves 8–15 μm long by 4.5–5 μm wide; striae 13–14 in 10 μm on both valves. Several of our specimens were smaller than usual for this taxon. It was most abundant in the concrete tub at 1.6% relative density.

Achnanthes linearis Grun., Figs. 19–20. Valves 8.5–15.5 μm long by 2–3 μm wide; striae 24–28 in 10 μm on both valves. Several of our specimens were smaller than typically observed for the nominate variety. A continuous range in length was observed so that we did not place our smaller specimens in *A. linearis* f. *curta*. This taxon showed preference for the stream, where it had a relative density of 1.3%. Very few specimens were observed in samples from the concrete tub.

Amphora cf. *coffeaeformis* (Ag.) Kuetz., Fig. 119. Valve 15 μm long by 3 μm wide; striae indistinctly punctate, 24 in 10 μm. This *Amphora* corresponds to the description of *A. coffeaeformis* sensu Patrick and Reimer (1975). However, it does not fit the taxon as reinterpreted by Archibald and Schoeman (1984). We saw only a single valve of this *Amphora*, which is common in some marshes surrounding the Great Salt Lake of Utah (Felix and Rushforth 1979, Squires et al. in press).

Amphora veneta Kuetz., Figs. 26–27. Valves 15–29 μm long 3–5 μm wide; striae 21–24 at midvalve, becoming 28–32 at the ends. This *Amphora* was somewhat more common in the tub, where it reached 1% relative density.

Anomoeoneis sphaerophora (Ehr.) Pfitz., Figs. 32–34. Valves 36.5–45 μm long by 10–14 μm wide; striae 18–20 in 10 μm. This taxon was present at both localities at about 7% relative density.

Caloneis ventricosa var. *truncatula* (Grun.) Meist., Fig. 31. Valve 36 μm long by 7μm wide; striae 18 in 10 μm. A single valve of this taxon was observed during our study.

Cocconeis placentula var. *lineata* (Ehr.) V.H., Fig. 18. Valves 17.5–23 μm long by 9–12 μm wide; striae 16–21 in 10 μm. This taxon was rare in our study and was found only in the concrete tub.

Cyclotella atomus Hust., Figs. 117–118. Valves 4–5 μm in diameter; striae 16–20 in 10 μm. This taxon was collected infrequently from both habitats.

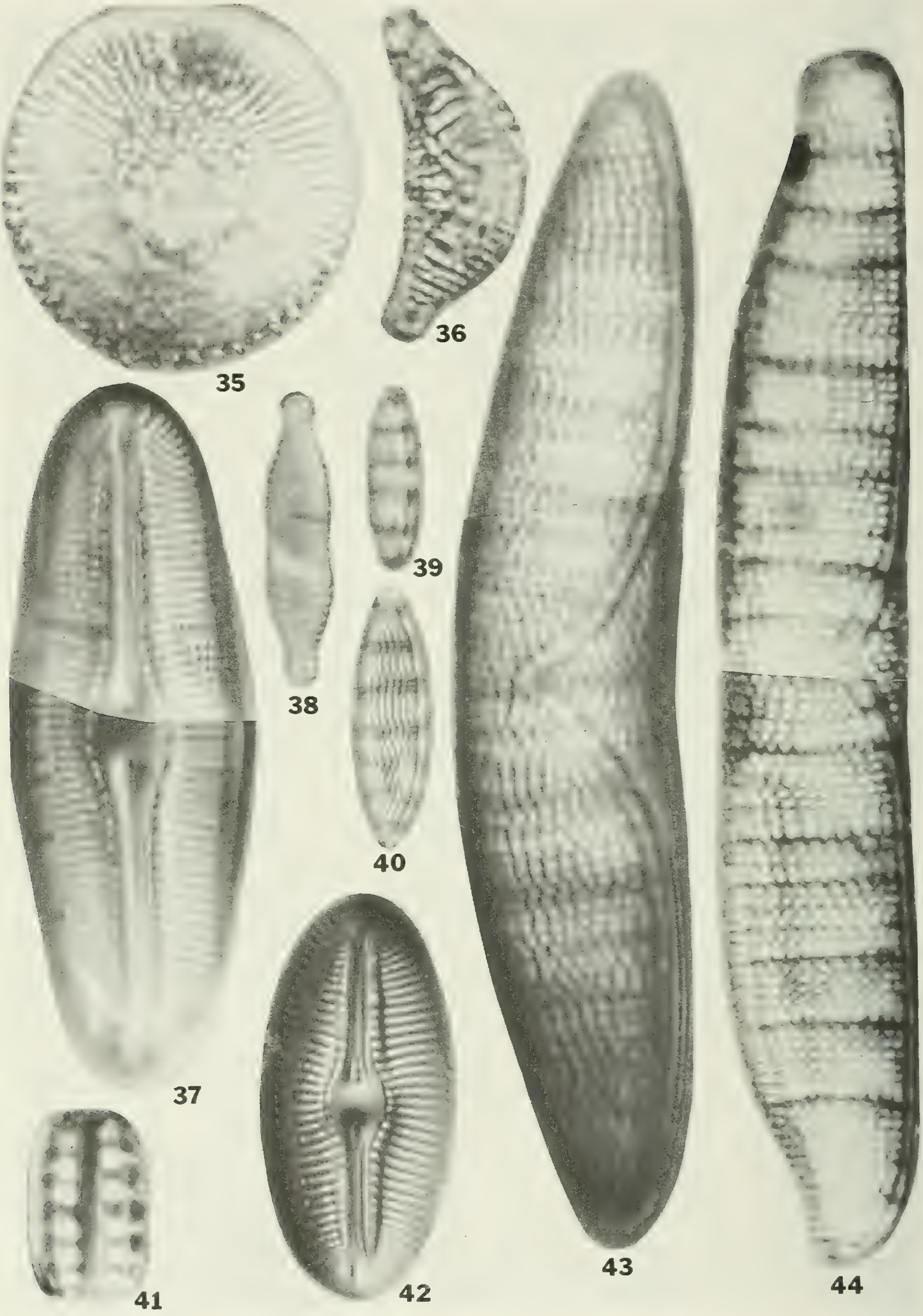
Cyclotella comta (Ehr.) Kuetz., Fig. 35. Valve 28 μm in diameter; striae 13–14 in 10 μm. A single valve of *C. comta* was observed.

Cyclotella meneghiniana Kuetz., Fig. 25. Valves 7.5–10 μm in diameter; striae 8–10 in 10 μm. Only two valves of this taxon were observed during our study.

Denticula elegans Kuetz., Figs. 39–41. Valves 10–31 μm long by 4–7 μm wide; costae 3–4 in 10 μm; striae 17–21 in 10 μm. *Denticula elegans* was less frequent in Cowboy Hot Tub than in many other thermal springs in western North America. It had a relative density of 2.4% in the concrete tub. It was present in the stream in lower numbers.

Denticula cf. *parva* Hust., Figs. 29–30. Valves 9–18.5 μm long by 3–3.5 μm wide; costae 6–10 in 10 μm; striae not resolved. We have seen this taxon in several spring systems throughout western North America. It was present in Cowboy Hot Spring in low numbers, always less than 1% relative density.

Diatoma hiemale var. *mesodon* (Ehr.) Grun., Fig. 28. Valve 17.5 μm long by 8.5 μm wide; costae 3 in 10 μm; striae 24 in 10 μm. Only a single valve of this taxon was observed.



Figs. 35–44. Diatom species: 35, *Cyclotella comta*; 36, *Epithemia sorex*; 37, *Diploneis oblongella*; 38, *Fragilaria construens* var. *binodis*; 39–41, *Denticula elegans*; 42, *Diploneis oblongella*; 43, *Epithemia argus*; 44, *Epithemia adnata* var. *porcellus*. All figures are 2000X.

Diploneis oblongella (Naeg. ex Kuetz.) Ross, Figs. 37, 42. Valves 31–52 μm long by 15–18 μm wide; striae 12–13 in 10 μm. Several valves were collected from both habitats during our study.

Epithemia adnata var. *porcellus* (Kuetz.) Patr., Fig. 44. Valve 90.5 μm long by 14 μm wide; costae 3 in 10 μm; striae 12 in 10 μm, 4–6 between costae. A single specimen of this taxon was observed.

Epithemia argus (Ehr.) Kuetz., Fig. 43. Valves 60–90 μm long by 12–16.5 μm wide; costae 2 in 10 μm; striae 10–11 in 10 μm, 4–6 between costae. This *Epithemia* was observed infrequently in samples from the concrete tub.

Epithemia sorex Kuetz., Fig. 36. Valve about 25 μm long by 9 μm wide; costae 12 in 10 μm; striae 2 between costae. Only a single frustule of this taxon was observed.

Fragilaria construens Grun., Fig. 45. Valves 10–15 μm long by 5.5 μm wide; striae 14 in 10 μm. Only two valves of this taxon were observed.

Fragilaria construens var. *binodis* (Ehr.) Grun., Fig. 38. Valve 22 μm long by 5 μm wide; striae 16 in 10 μm. A single valve of this taxon was observed during our study.

Fragilaria construens var. *venter* (Ehr.) Grun., Figs. 46–48. Valves 5.5–10 μm long by 4–4.5 μm wide; striae 12–16 in 10 μm. This taxon was quite rare in our study, always less than 1% relative density.

Fragilaria lapponica Grun., Fig. 53. Valve 32 μm long by 6 μm wide; striae 10–12 in 10 μm. A single valve of this taxon was observed.

Fragilaria pinnata var. *lancettula* (Schum.) Hust., Fig. 52. Valve 20 μm long by 6 μm wide; striae 10 in 10 μm. A single valve of this diatom was observed.

Fragilaria similis Krasske, Fig. 51. Valve 15 μm long by 5 μm wide; striae 10 in 10 μm. A single valve of *F. similis* was observed.

Gomphonema gracile Ehr., Figs. 58–60. Valves 24–32.5 μm long by 6.5–7.5 μm wide; striae 12–16 in 10 μm. It was present in low numbers in Cowboy Hot Spring, always less than 1% relative density.

Gomphonema parvulum Kuetz., Figs. 49–50. Valves 16–17.5 μm long by 4.5–5 μm wide; striae 14 in 10 μm. Two frustules of this *Gomphonema* were observed during our study.

Navicula confervacea (Kuetz.) Grun., Figs. 73–74. Valves 18–26 μm long by 7–8 μm wide; striae 19–24 in 10 μm. This taxon was present in samples from both sites in low numbers, always less than 1% relative density.

Navicula confervacea var. *peregrina* (W. Sm.) Grun., Figs. 69–71. Valves 6–13 μm long by 3.5–4 μm wide; striae 24 in 10 μm. Specimens of this variety were somewhat smaller than generally observed. It was present at about the same density as the nominate in samples from both sites.

Navicula cincta (Ehr.) Ralfs, Figs. 54–57. Valves 14–24.5 μm long by 4–5.5 μm wide; striae 14–16 in 10 μm. Our specimens of this taxon differ from the typical by being smaller with somewhat coarser striae. This diatom was present in rather high numbers, reaching 11.0% relative density in the thermal stream.

Navicula cryptocephala var. *veneta* (Kuetz.) Rabh., Figs. 65–68. Valves 18–26 μm long by 5.5–6.5 μm wide; striae 14–16 in 10 μm. This *Navicula* was present in the concrete pool at 2.2% relative density and 1% relative density in the thermal stream.

Navicula halophila (Grun.) Cl., Figs. 63–64. Valves 34–53 μm long by 10–12.5 μm wide; striae 16–20 in 10 μm. This *Navicula* was more common in the stream, where it reached nearly 2% relative density.

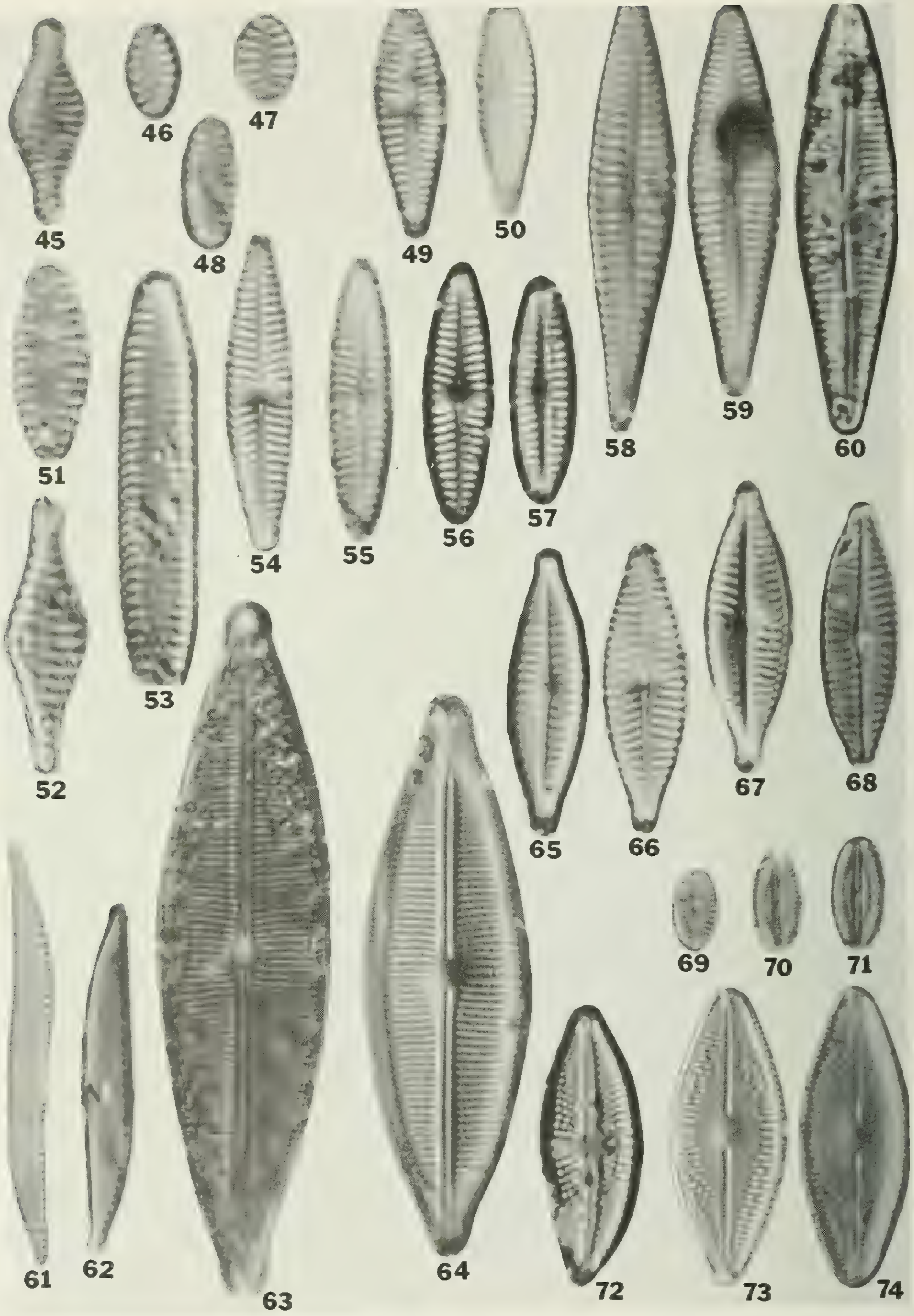
Navicula mutica Kuetz., Fig. 72. Valve 21 μm long by 7.5 μm wide; striae 18 in 10 μm. A single valve of this taxon was observed.

Nitzschia clausii Hantz., Figs. 61–62. Valves 25.5–36.5 μm long by 3–4.5 μm wide; striae not resolved; fibulae 13–16 in 10 μm. Fibulae of our specimens were somewhat finer than previously reported for this taxon. It was present at less than 1% relative density in both sampling localities.

Nitzschia communis Rabh., Figs. 77–79. Valves 20–38.5 μm long by 4–5 μm wide; striae approximately 32–36 in 10 μm, often unresolved; fibulae 10–16 in 10 μm. It was present at 4% relative density in both the concrete tub and the spring stream.

Nitzschia frustulum (Kuetz.) Grun., Figs. 82–85. Valves 8–22 μm long by 3–4 μm wide; striae 21–22 in 10 μm; fibulae 10–12 in 10 μm. This *Nitzschia* was one of the most common diatoms in our study. It occurred at 32% relative density in the concrete tub and as high as 30% relative density in the runoff stream.

Nitzschia frustulum var. *subsalina* Grun., Figs. 89–90. Valves 13–20 μm long by 2.5–3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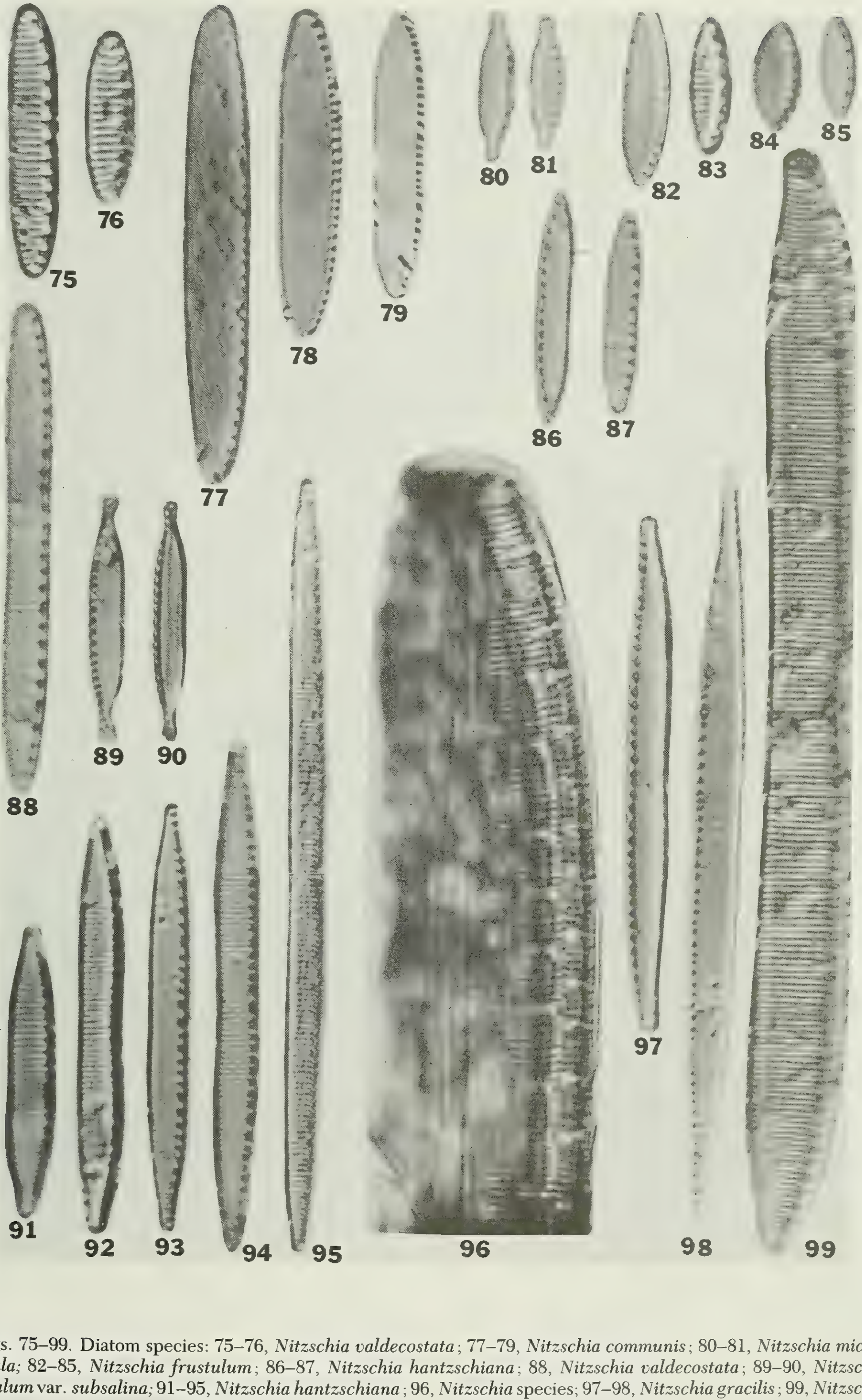
Figs. 45–74. Diatom species: 45, *Fragilaria construens*; 46–48, *Fragilaria construens* var. *venter*; 49–50, *Gomphonema parvulum*; 51, *Fragilaria similis*; 52, *Fragilaria pinnata* var. *lancettula*; 53, *Fragilaria lapponica*; 54–57, *Navicula cincta*; 58–60, *Gomphonema gracile*; 61–62, *Nitzschia clausii*; 63–64, *Navicula halophila*; 65–68, *Navicula cryptocephala* var. *veneta*; 69–71, *Navicula confervacea* var. *peregrina*; 72, *Navicula mutica*; 73–74, *Navicula confervacea*. All figures are 2000X.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Figs. 75–99. Diatom species: 75–76, *Nitzschia valdecostata*; 77–79, *Nitzschia communis*; 80–81, *Nitzschia microcephala;* 82–85, *Nitzschia frustulum*; 86–87, *Nitzschia hantzschiana*; 88, *Nitzschia valdecostata*; 89–90, *Nitzschia frustulum* var. *subsalina;* 91–95, *Nitzschia hantzschiana*; 96, *Nitzschia* species; 97–98, *Nitzschia gracilis*; 99, *Nitzschia heufleriana*. All figures are 2000X.

μm wide; striae 32 in 10 μm; fibulae 14–15 in 10 μm. Several valves of this taxon were observed in both the concrete tub and the thermal stream.

Nitzschia gracilis Hantz., Figs. 97–98. Valves 40.5–62.5 μm long by 3–3.5 μm wide; striae 32–33 in 10 μm, often unresolved; fibulae 11–14 in 10 μm. This taxon was present in samples from both collecting sites at a relative density of less than 1%.

Nitzschia hantzschiana Rabh., Figs. 86–87, 91–95. Valves 10.5–60 μm long by 2–3.5 μm wide; striae 22–24 in 10 μm; fibulae 10–13 in 10 μm. Our collections of this taxon contain specimens that are both shorter and longer than generally reported. However, a good size gradient was observed. This taxon occurred between 9% and 10% relative density in both the concrete tub and the stream.

Nitzschia heufleriana Grun., Fig. 99. Valve 85 μm long by 7 μm wide; striae 20 in 10 μm; fibulae 10 in 10 μm. We saw a single specimen of this *Nitzschia* that had ends less capitate than usual.

Nitzschia microcephala Grun., Figs. 80–81. Valves 8.5–11.5 μm long by 2.5–3 μm wide; striae unresolved; fibulae 10–14 in 10 μm. This taxon reached 1% relative density in the thermal stream but was absent in the concrete tub.

Nitzschia valdecostata Lange-Bert. and Simon., Figs. 75–76, 88. Valves 13–37.5 μm long by 3.5–4.5 μm wide; striae 16–18 in 10 μm; fibulae 7–9 in 10 μm. We used the epithet *N. valdecostata* rather than *N. valdestriata* since our specimens appeared to lack a nodulus. Petersen (1930) has also collected this taxon (as *N. valdestriata*) from thermal waters. This *Nitzschia* occurred in the concrete tub at about 2% relative density and about 3% relative density in the stream.

Nitzschia species, Figs. 96, 114. Valves linear, greater than 100 μm long by 8 μm wide; striae 17–20 in 10 μm; fibulae 3 in 10 μm. This *Nitzschia* has been seen in several California thermal springs but has never been abundant in any of our samples. At Cowboy Hot Spring it was present in both the concrete tub and the spring stream in low numbers.

Pinnularia appendiculata (Ag.) Cl., Figs. 102–104. Valves 18.5–25 μm long by 4.5–6 μm wide; striae 20–22 in 10 μm. Some specimens demonstrated more strongly radiate striae near midvalve (Figs. 103–104) than others. However, it appeared that this feature intergraded in the population. This taxon was more common in the stream but occurred at less than 1% relative density.

Pinnularia intermedia (Lagerst.) Cl., Figs. 107–109. Valves 11.5–17 μm long by 3–3.5 μm wide; striae 10–12 in 10 μm. Our specimens were shorter than usual for this taxon. Some of our specimens were similar to *P. obscura* since they had up to 12 striae in 10 μm. This diatom was rare in our samples.

Pinnularia microstauron (Ehr.) Cl., Figs. 111–113. Valves 24–52 μm long by 7–13 μm wide; striae 10–12 in 10 μm. Some of our specimens are very similar to *P. brebissonii*. However, since they seemed to be at one end of a morphological gradient from the more common and more typical *P. microstauron* specimens, we opted to use the latter specific name. This taxon was not particularly common, although a number of frustules were collected.

Pinnularia stauroptera var. *recta* (May.) Cleve-Euler, Fig. 110. Valve 43 μm long by 7.5 μm wide; striae 9 in 10 μm. Hustedt (1930) used *Pinnularia gibba* var. *linearis* for specimens similar to ours. A single specimen of this taxon was observed in a sample from the thermal stream.

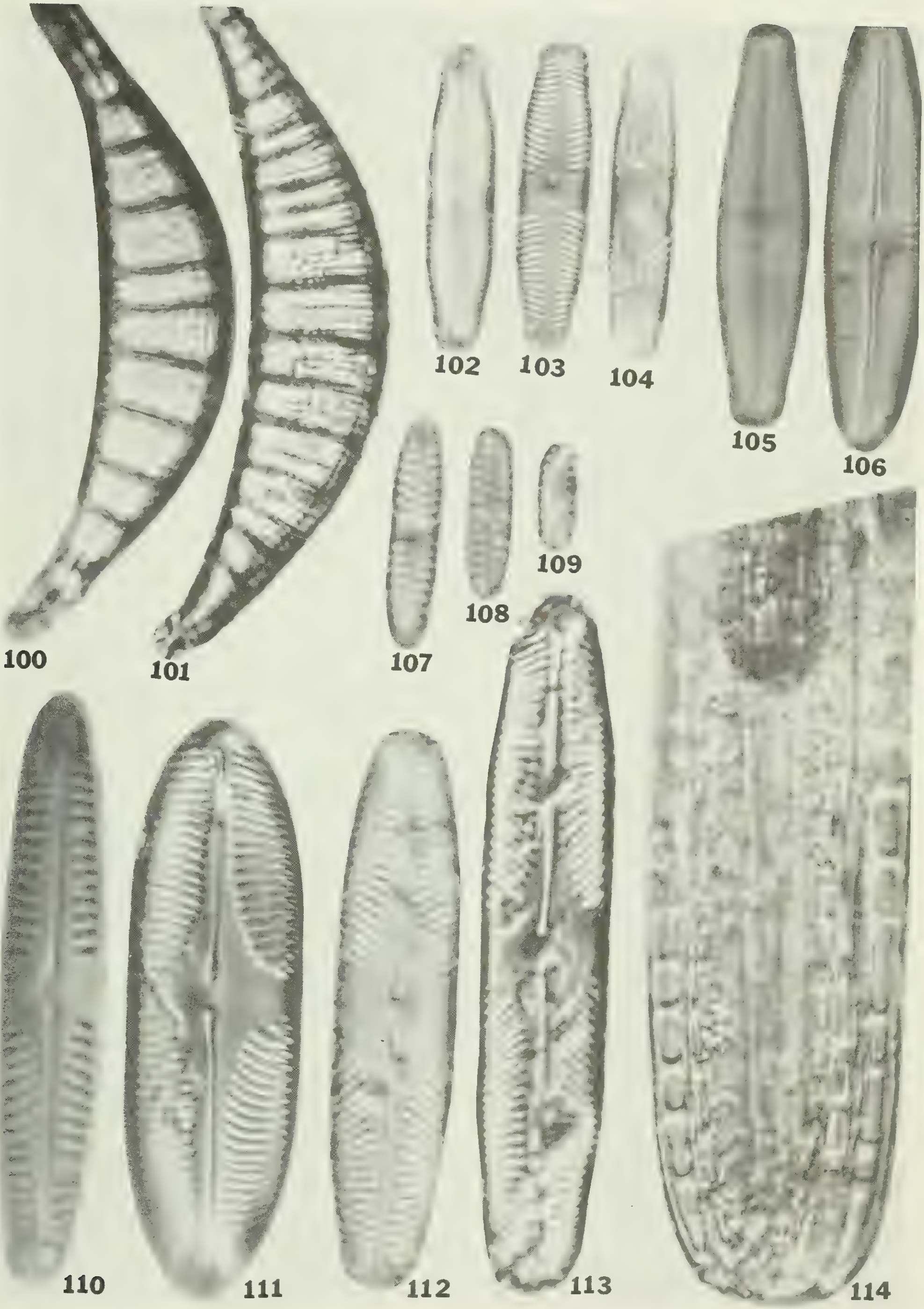
Rhopalodia gibberula (Ehr.) O. Muell., Fig. 115. Valve 80–127.5 μm long by 12–12.5 μm wide; striae 18 in 10 μm; costae 3–5 in 10 μm. It was rare in the concrete tub.

Rhopalodia operculata (C. A. Ag.) Hakansson, Fig. 100–101, 120. Valves 25–49 μm long; 6–12 μm wide; striae 18–20 in 10 μm; costae 3–6 in 10 μm. This taxon occurred in samples from the concrete tub at 2% relative density and was somewhat rarer in the stream.

Stauroneis wislouchii Poretz. et Anisimowa, Figs. 105–106. Valves 22–34 μm long by 5–8 μm wide; striae 22–26 in 10 μm. This taxon was present in samples from both collecting localities at about 0.5% relative density.

Stephanodiscus carconensis var. *pusilla* Grun., Fig. 124. Valves 26–28 μm in diameter; large striae 4 in 10 μm, composed of distinct rows of punctae; rows of punctae 17–18 in 10 μm. Only two valves of this taxon were found in our samples.

Surirella ovalis Breb., Fig. 116. Valve 113 μm long by 53 mm wide; striae 14 in 10 μm;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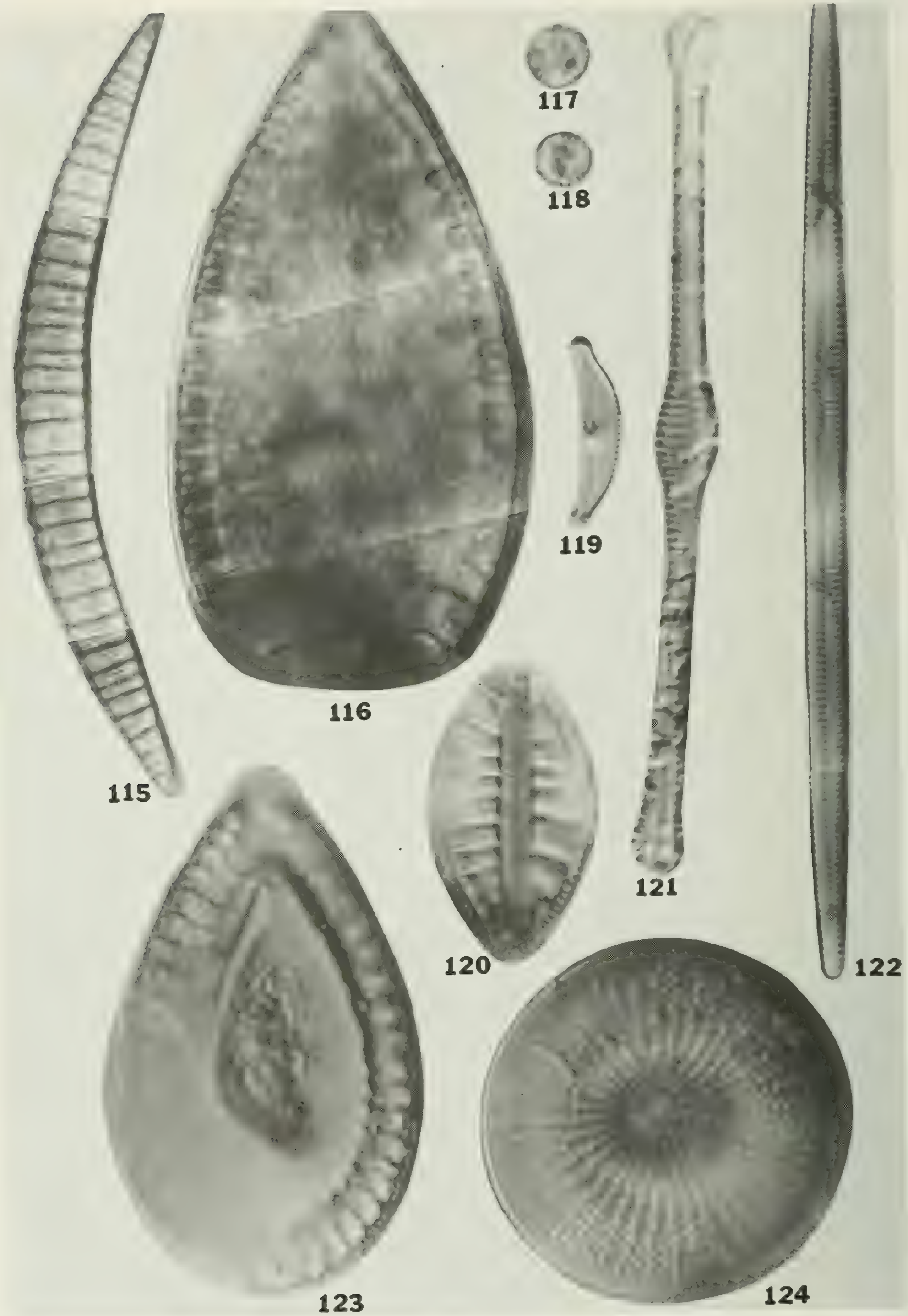
Figs. 100–114. Diatom species: 100–101, *Rhopalodia operculata*; 102–104, *Pinnularia appendiculata*; 105–106, Stauroneis wislouchii; 107–109, *Pinnularia intermedia*; 110, *Pinnularia stauroptera* var. *recta*; 111–113, *Pinnularia microstauron*; 114, *Nitzschia* species. All figures are 2000X.



Figs. 115–124. Diatom species: 115, *Rhopalodia gibberula*; 116, *Surirella ovalis*; 117–118, *Cyclotella atomus*; 119, *Amphora* cf. *coffeaeformis*; 120, *Rhopalodia operculata*; 121, *Tabellaria quadrisepta*; 122, *Synedra ulna*; 123, *Surirella ovalis* var. *brightwellii*; 124, *Stephanodiscus carconensis* var. *pusilla*. Figures 115, 116 and 122 are 1000X. All others are 2000X.

wing canals 3 in 10 μm. Only a single specimen of this taxon was observed in our samples.

Surirella ovalis var. *brightwellii* (W. Sm.) Cl., Fig. 123. Valves 39 μm long by 21–23 μm wide; striae 19–20 in 10 μm; wing canals 5–6 in 10 μm. Only two specimens of this taxon were observed in our samples.

Synedra ulna (Nitz.) Ehr., Fig. 122. Valve 115 μm long by 6.5 μm wide; striae 10 in 10 μm. This taxon occurred as a single specimen from the concrete tub.

Tabellaria quadrisepta Knuds., Fig. 121. Valves 37–65 μm long by 6 μm wide at midvalve; striae 15–16 in 10 μm. Only three frustules of this taxon were observed in our samples.

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INVENTORY OF UTAH CRAYFISH WITH NOTES ON CURRENT DISTRIBUTION

James E. Johnson[1]

ABSTRACT.—Crayfish distribution and composition in Utah are poorly documented. Based upon limited collections, the native *Pacifastacus gambelii* is widespread and often abundant in the Bear and Weber river drainages and is occasionally represented in smaller tributaries to the Great Salt Lake and to the Raft River. *Pacifastacus leniusculus* was collected from Utah County and *Procambarus clarkii* from Tooele County; the origin of these populations is not known. The nonnative crayfish *Orconectes virilis* is currently abundant in the Virgin, Price, and Duchesne river basins and the Glen Canyon, Flaming Gorge, Deer Creek, and Starvation reservoirs; it is expanding in Huntington North, Scofield, and Willard reservoirs. Further work is required to develop a more complete inventory and monitor the impacts on aquatic ecosystems of expanding nonnative crayfish populations. Surreptitious stockings can be dealt with only if the public is made aware of the adverse consequences of ill-conceived introductions.

Crayfish, as listed in Hobbs (1976), are represented in Utah by only one native species, *Pacifastacus* (*Hobbsastacus*) *gambelii* (Girard 1852), and that only north of approximately Salt Lake county (personal observation). Apparently crayfish are not native to the Green–Colorado River system (Dean 1969) or to that portion of the Bonneville Basin, including the Sevier River drainage, south of approximately Utah County (personal observation). Two other species of *Pacifastacus* are native to waters adjoining Utah, *Pacifastacus* (*Pacifastacus*) *leniusculus* (Dana 1852) in Nevada and *Pacifastacus* (*Hobbsastacus*) *connectens* (Faxon 1914) in Idaho (Pennak 1978) and may be native to Utah waters; however, this possibility has yet to be confirmed. *Pacifastacus leniusculus* is present in Utah County but may have been introduced there. The introduction of *Orconectes virilis* (Hagen 1870) has resulted in burgeoning populations of this nonnative in several of Utah's major drainages in recent years. One isolated population of *Procambarus* (*Scapulicambarus*) *clarkii* (Girard 1852) is found in Tooele County, probably also representing an introduction.

Crayfish feed on vegetation, and certain species have been shown to control nuisance aquatic plants (Dean 1969). They also feed on detritous and are considered important components of food webs supplying certain fisheries (Jones and Momot 1981). Their food habits and importance as food for man and as prey for various species of sportfish have led to the widespread introduction of certain crayfish species. Since approximately 1950 *Orconectes virilis*[2] has been stocked in the Colorado River watershed of western New Mexico and northeastern Arizona, primarily for vegetation control (Dean 1969). During 1967, 1968, and 1970, *O. virilis* were collected by Utah Division of Wildlife Resources (UDWR) personnel from Nogal Lake in south central New Mexico, Red Lake on New Mexico's Navajo Indian Reservation, and the Little Colorado River of Arizona. These crayfish were stocked in the Sand Cove reservoirs (upper Santa Clara River drainage of the Virgin River) and Pelican Lake, Walls, Vernal Golf Course, Rasmussen and Stringham ponds (in the Vernal, Utah, area, Duchesne River drainage), and in a golf course pond adjacent to the Price River near Price, Utah. Prior to 1968 the U.S. Fish and Wildlife Service (USFWS) had planted *O. virilis* in Towave and Midway reservoirs, Uinta Indian Reservation (also Duchesne drainage).

Crayfish were reported to be a prominent food of largemouth bass at Glen Canyon Reservoir, Utah-Arizona, shortly after its impoundment (May et al. 1975), and the presence of crayfish in Flaming Gorge Reservoir, Utah-Wyoming, was confirmed during the 1970s. In neither case was the species of crayfish identified.

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[2] In the opinion of Horton H. Hobbs, Jr., Smithsonian Institution, Washington, D.C., *Orconectes causeyi* (Jester 1967) is a synonym of *O. virilis* (personal communication, 1984). *Orconectes virilis* and *O. causeyi* are, therefore, collectively referred to as *O. virilis* in this paper.

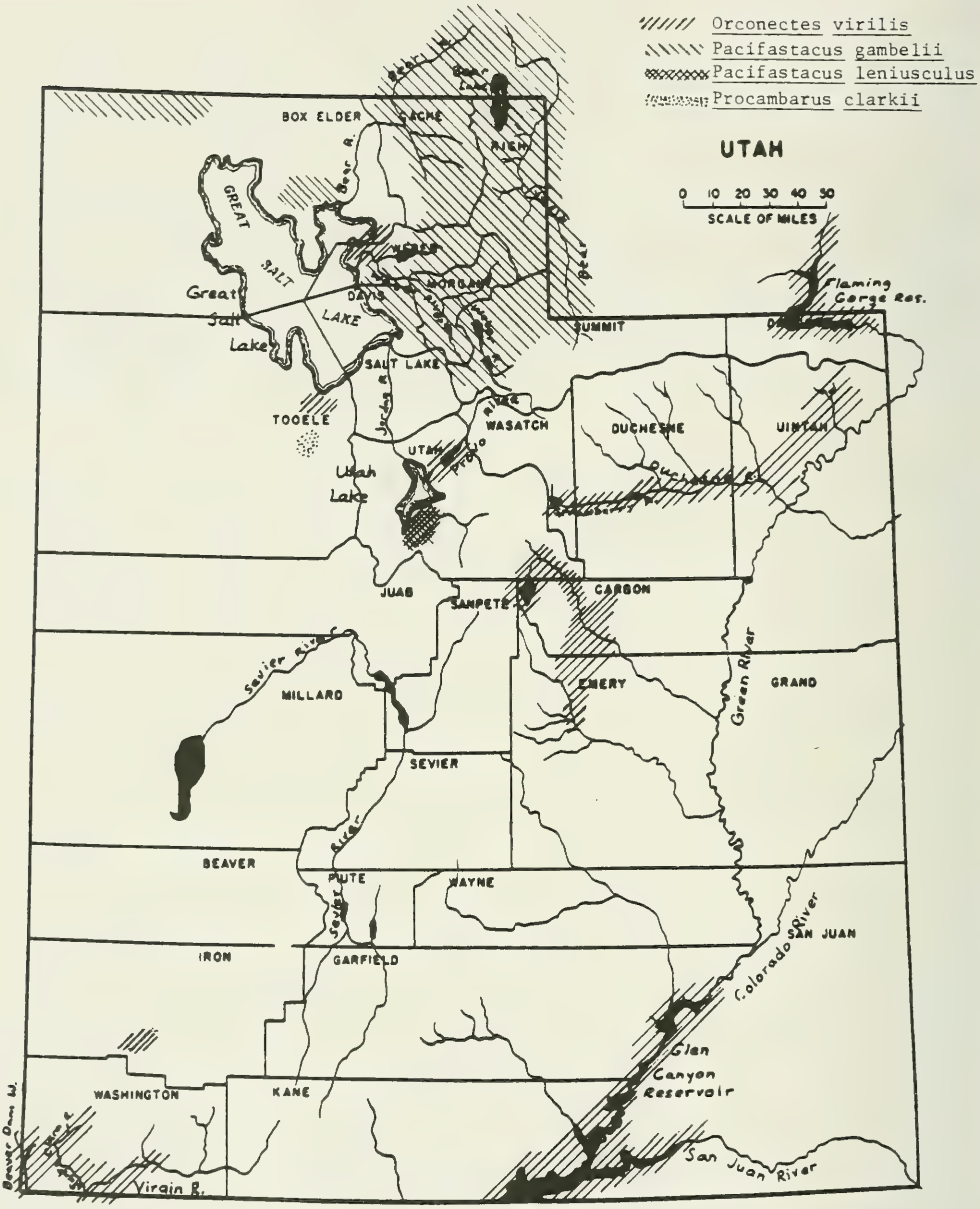
Orconectes virilis
Pacifastacus gambelii
Pacifastacus leniusculus
Procambarus clarkii
UTAH
0 10 20 30 40 50
SCALE OF MILES
BOX ELDER
CACHE
RICH
Bear R.
Bear Lake
GREAT SALT LAKE
Great Salt Lake
WEBER
DAVIS
MORGAN
SUMMIT
DAGGETT
Flaming Gorge Res.
SALT LAKE
Jordan R.
TOOELE
WASATCH
Provo River
UTAH
Utah Lake
DUCHESNE
Duchesne R.
Strawberry R.
UINTAH
JUAB
SANPETE
CARBON
Sevier River
MILLARD
EMERY
Green River
GRAND
SEVIER
BEAVER
PIUTE
WAYNE
Sevier R.
SAN JUAN
Colorado River
IRON
GARFIELD
Glen Canyon Reservoir
WASHINGTON
KANE
Beaver Dam W.
Virgin R.
San Juan River

Fig. 1. Approximate current distribution of crayfish in Utah, based upon UDWR fishery collections made from 1978 to 1984.

The distribution of crayfish has spread rapidly since 1975, although the UDWR made no successful introductions after July 1977, when the Fisheries Section imposed a moratorium on further stockings. Anglers, however, observed the importance of crayfish in the diets of game fish at Lake Powell and other waters, and it is suspected that this knowledge led to a rash of surreptitious plantings of crayfish by the public in additional drainages. (It is unlawful in Utah for anglers to transport live fish for bait; therefore, the bait-bucket is probably not a significant vector of crayfish in Utah.) Furthermore, previous introductions had resulted in some dense populations that were spontaneously spreading within their drainages.

The purpose of this paper is to contribute to

TABLE 1. Crayfish collection sites by UDWR fishery personnel, from which preserved specimens were made available to the author, 1978–1984.

Drainage	Site	Collection date	Collector	Species
COLORADO				
Virgin River	Lower Sand Cove	1982	D. Hepworth and J. Leppink	*Orconectes virilis*
	Gunlock	1983	D. Hepworth	*Orconectes virilis*
	Beaver Dam Wash	3 July 1984	W. Gustaveson	*Orconectes virilis*
Glen Canyon Reservoir	Wahweap Bay	Composite of 1982 and 1983	W. Gustaveson	*Orconectes virilis*
	San Juan Arm	Composite of 1982 and 1983	W. Gustaveson	*Orconectes virilis*
	Bullfrog Bay	Composite of 1982 and 1983	W. Gustaveson and S. Scott	*Orconectes virilis*
Flaming Gorge Reservoir	Near Dam	October 1982	S. Brayton	*Orconectes virilis*
Starvation Reservoir	Boat Ramp	September 1983	M. Ottenbacher and S. Scott	*Orconectes virilis*
Price River Drainage	Scofield Reservoir	September 1984	W. Donaldson	*Orconectes virilis*
GREAT SALT LAKE				
Provo River	Deer Creek Reservoir	21 August 1981	D. Sakaguchi	*Orconectes virilis*
Weber River	Willard Reservoir Morgan-Peterson	7 December 1982 16 September 1982	J. Leppink J. Leppink	*Orconectes virilis* *Pacifastacus gambelii*
Lost Creek	Lost Creek Reservoir	12 August 1984	J. Johnson	*Pacifastacus gambelii*
Bear River	Wellsville and Hyrum reservoirs	September 1982	T. St. John	*Pacifastacus gambelii*
Bear River	Bear Lake	Several	B. Nielson	*Pacifastacus gambelii*
Bear River	Big Creek	1982	J. Leppink	*Pacifastacus gambelii*
Great Salt Lake	Salt Creek	5 September 1984	K. Summers	*Pacifastacus gambelii*
Utah Lake	Salem Pond	1981	D. Sakaguchi	*Pacifastacus leniusculus*
Utah Lake	Spring Pond	1981	D. Sakaguchi	*Pacifastacus leniusculus*
COLUMBIA RIVER				
Raft River	Cotton-Thomas Basin	17 August 1984	J. Leppink	*Pacifastacus gambelii*
WESTERN BASINS	Rush Valley near St. John	1978 and 17 August 1983	D. Sakaguchi	*Procambarus clarkii*

the current inventory of the distribution of crayfish in Utah and to serve as a baseline for future studies. The information presented is not comprehensive; sampling was largely by convenience rather than design, and large areas, especially Utah's western basins, were not sampled.

METHODS

All UDWR fishery biologists were asked to preserve in formalin all crayfish collected incidental to scheduled fish sampling. Thus, specimens were collected primarily with gill nets and electrofishing gear. In addition, some specimens were collected by hand from the substrate rubble and using baited lift nets and cage traps. Specimens were labeled as to capture site, date, and method and sent to the author for identification. Collection sites, therefore, largely represent waters under public sportfishery management programs. Very few collection efforts were made on fishless waters.

Tentative identification was made using keys of Hobbs (1976) and Pennak (1978). Samples of each species identified, with the exception of *Pacifastacus leniusculus*, were sent to

H. H. Hobbs, Jr., Department of Invertebrate Zoology, U.S. National Museum of Natural History, Smithsonian Institution, Washington, D. C., for confirmation of my tentative identification.

RESULTS

Colorado–Green River Drainage

Although not endemic, crayfish are now widespread in the Utah portion of the Colorado–Green River drainage. All specimens collected to date have been *Orconectes virilis* (Fig. 1, Table 1). The species is abundant in Flaming Gorge and Glen Canyon reservoirs and in the Virgin and Duchesne drainages but has not appeared in fish collections from the San Juan, White, Yampa, Green, or Colorado rivers within Utah. It has, however, been collected from the Colorado River upstream of approximately Grand Junction, Colorado (Unger 1978).

Crayfish were apparently absent until very recently in the Strawberry River above Soldier Creek Dam, based upon their absence from extensive UDWR fish sampling of Soldier Creek and Strawberry reservoirs and their tributaries. Anglers have reported, however, that crayfish are now present in Soldier Creek Reservoir.

Reports have been received of the presence of *O. virilis* from Scofield and Huntington North reservoirs and the Price River. A specimen from Scofield Reservoir, sent to me for verification by W. Donaldson (UDWR Southeastern Regional office, Price, Utah, November 1984), proved to be *O. virilis*.

Great Salt Lake Drainage

If crayfish were native to the Provo River drainage, the species should have been *Pacifastacus gambelii*, the documented native of the Bonneville basin (Hobbs 1972). No specimens of *P. gambelii* from the Provo River have come to my attention; however, *O. virilis* began appearing in fish sampling gear in 1981 at Deer Creek Reservoir. By 1984 they were abundant at Deer Creek Reservoir and were reported to have been seen in the Provo River downstream of Deer Creek Dam (Sakaguchi 1984).

Orconectes virilis was collected from the inlet of Willard Reservoir, a freshwater impoundment on the Bear River arm of the Great Salt Lake, in November 1982. The collection site was below a large drop structure that may serve as a barrier to upstream migration of crayfish to the Weber River. I have also identified this species in Stansbury Park Lake in Tooele County near the south shore of the Great Salt Lake. These populations apparently initiated with surreptitious stockings.

Pacifastacus gambelii is native and widespread in the Ogden/Weber drainage. They were collected in abundance from the Weber River at Morgan in 1982 and from Lost Creek Reservoir in 1984. Crayfish have been observed by UDWR personnel in Rockport, Echo, and East Canyon reservoirs. With the exception of Willard Reservoir, only *P. gambelii* has been identified from the Weber drainage to date.

All collections to date from the Bear River have been identified as *Pacifastacus gambelii* (Table 1). The species is widespread and occasionally very abundant. No UDWR collections of crayfish have been made from the Bear River upstream of approximately the Woodruff Narrows. Wyoming Game and Fish Department personnel (W. Wengert, Green River, Wyoming, personal communication, 1984) have observed crayfish in Woodruff Narrows, Huff Creek, and Salt Creek, of the Bear River drainage. These specimens were not identified but were very likely *P. gambelii*.

Pacifastacus gambelii is abundant in Salt Creek, a tributary to the North Arm of the Great Salt Lake. Other tributaries to the North Arm contain crayfish but have not been inventoried.

Specimens from Salem and Spring ponds near Payson, Utah County, Utah, collected by D. Sakaguchi, were tentatively identified as *Pacifastacus leniusculus*, native to California, Oregon, Idaho, Washington, and Nevada (Pennak 1978).

The author has been informed of observations of crayfish and shallow burrows in wetlands surrounding Utah Lake, but no specimens have been collected.

Raft River (Columbia) Drainage

Although comparatively little effort has been expended searching for crayfishes in the Raft River basin of the Columbia Drainage, *Pacifastacus gambelii* has been collected from two small tributaries (Table 1) and is thought to be present elsewhere in the Raft River drainage.

Western Basins and Sevier River Drainages

Crayfish have not been observed during extensive samplings of the Pilot or Deep Creek Mountain drainages; nor have crayfish been collected from western basin natural lakes and wetlands.

Orconectes virilis has appeared in Newcastle Reservoir in southern Iron County, apparently from sources in the adjacent Santa Clara River drainage (D. Hepworth, UDWR, personal communication, 1984).

Specimens collected by D. Sakaguchi, UDWR, from a warm spring in Rush Valley, Tooele County, in 1978 and 1983 were identified by H. Hobbs, Jr. (U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C.) to be *Procambarus clarkii*, a species common in the south central United States (Pennak 1978).

No crayfish have been reported from anywhere within the Sevier drainage. Crayfish may not be endemic to this area and, apparently, have not yet been introduced.

DISCUSSION

Colorado River Drainage

The presence of *Orconectes virilis* in the Colorado River drainage is probably the result of a number of introductions. The Santa Clara River populations originated with the UDWR introduction in 1970 at Sand Cove Reservoir in the upper Santa Clara drainage. This introduction was followed by observations of crayfish in Gunlock (1978) and Ivans (1980) reservoirs and the lower Santa Clara River and upstream through Baker Reservoir (1978). In 1983 *O. virilis* was collected from ponds along the East Fork of Beaver Dam Wash. In the Virgin River and Ash Creek, *O. virilis* is currently distributed upstream to approximately La Verkin and Toquerville, respectively. *Procambarus clarkii* is common in Lake Mead and therefore has access to the Virgin River. No. *P. clarkii* have been sampled to date from the Virgin drainage of Utah, however.

The origin of *Orconectes virilis* in Glen Canyon Reservoir is less clear. One surreptitious plant of *O. virilis* is believed to have occurred in 1965; but crayfish were known to be present in the reservoir as early as 1964 (May et al. 1975). Evidently *O. virilis* was present in the drainage at the time of impoundment or was introduced accidentally with game fish, many of which were obtained from midwestern hatcheries.

The apparent absence of crayfishes in Utah waters of the mainstem Colorado and Green rivers and the San Juan River upstream of Lake Powell deserves attention. *Orconectes virilis* now has access from both upstream and downstream and may colonize these reaches and eventually populate the White, Yampa, and other tributaries, all with unique native fish populations. *Orconectes virilis* generally occurs in relatively clear waters with stony bottoms (Pennak 1978) and may therefore prove intolerant of the Colorado system's silt-laden reaches.

The UDWR and USFWS introductions in the Uinta Basin during the period 1965–1968 resulted, by approximately 1975, in dense populations of *Orconectes virilis* in Bottle Hollow, Midview (Boreham), and numerous smaller reservoirs, as well as in the Duchesne River from its mouth upstream at least through the City of Duchesne. Although abundant in the water supply of Pelican Lake, the species has not become established in Pelican. Between 1980 and 1984 *O. virilis* appeared in Steinaker and Starvation reservoirs. The upstream extent of the current distribution of *O. virilis* in Duchesne River tributaries is presently poorly documented. The UDWR introduction in a golf course pond near Price was probably the source of the lower Price River and Huntington North Reservoir populations, but the crayfish in Scofield Reservoir probably resulted from surreptitious stockings.

Crayfish were probably absent from Flaming Gorge Reservoir and its drainage at the time of impoundment. Wyoming Game and Fish Department planted *Pacifastacus gambelii* in the Green River, between Flaming Gorge and Fontenelle reservoirs, in 1965 and 1966. The source of these crayfish was the Teton Valley Ranch near Jackson, in the Snake River drainage. In 1974 Wyoming planted largemouth bass into Flaming Gorge from Springer Pond, south of Buffalo, Wyoming. A few small crayfish were captured and stocked incidentally with the bass. The crayfish of Springer Pond have been identified by Wyoming Game and Fish Department (W. Wengert, Green River, Wyoming, personal communication 1984) as *Orconectes virilis*. Fish hatcheries with dirt ponds often harbor crayfish, and a variety of such hatcheries, some located within the native range of *O. virilis*, have contributed to the stocking of Flaming Gorge Reservoir over the years. This species is now abundant in Flaming Gorge Reservoir. It is the primary source of prey for the reservoir's smallmouth bass population and contributes to the diets of lake trout, brown trout, and rainbow trout (Pettengill et al. 1984).

Great Salt Lake Drainage

Pacifastacus gambelii has not been collected from Willard Reservoir; the Weber River downstream of approximately Peterson, Utah; or the Bear River from Cutler Reservoir downstream to the Great Salt Lake. Their apparent absence from these warmer waters suggests this species may be intolerant of warmer waters or of warm water fish populations. It has not been collected from the Ogden River drainage, possibly because fish toxicants were used in the reclamation of the fisheries of Pineview and Causey reservoirs.

The population of *Orconectes virilis* in Willard Reservoir is at the lower extreme of the Weber drainage. Confined by salt water downstream and a drop structure in the inlet canal, this species may not have access to the lower Weber River. If *O. virilis* succeeds in reaching the river, it can be expected to spread rapidly upstream, in a manner similar to its rapid colonization of the Duchesne and Price rivers. Furthermore, it is possible the native species will become extirpated or reduced in number in much of the Salt Lake drainage, such as occurred to native species following *O. virilis* introductions in Maryland (Schwartz et al. 1963), Tennessee, West Virginia, Mississippi (Bouchard 1976), and possibly California (Bouchard 1977, Eng and Daniels 1982). *Orconectes virilis* is a very successful and aggressive species (Bouchard 1977) and could well displace Utah's native species (H. Hobbs, Jr., personal communication, 1984). Because of the tendency of anglers to transplant crayfish, and the availability of *O. virilis* in several popular fishing waters, including Deer Creek, Flaming Gorge, and Glen Canyon reservoirs, further appearances of *O. virilis* can be expected in waters attractive to anglers.

Only one specimen of *Pacifastacus leniusculus* each was collected from Salem and Spring ponds, Utah County. This species is clearly not as abundant or widespread as *P. gambelii*, and its origin in Utah is uncertain. If native, discovery of further populations in the Payson–Spanish Fork area, and perhaps in the western basins, can be expected.

Raft River (Columbia) Drainage

Pacifastacus connectens is reported to be native to Idaho and northern Utah (Eng and Daniels 1982). The specimens collected in the Raft River drainage proved to be *P. gambelii*, however, and no specimens of *P. connectens* have as yet come to my attention. If *P. connectens* is indeed represented in Utah, it might be expected to be present in the Columbia drainage. All future specimens from this drainage should be closely inspected; both *P. connectens* and *P. gambelii* have dorsal patches of setae on the palm of the chela, and a cursory inspection could therefore result in misidentification.

Western Basins and Sevier River Drainages

The waters of western Utah, within the Bonneville basin, are largely uninventoried with respect to crayfish. The only crayfish populations recorded in this area would appear to be *Orconectes virilis* in Newcastle Reservoir at the southern extreme of the basin, first observed in 1980 (the result of surreptitious stocking), and the population of *Procambarus clarkii* in a small warm spring near St. John in Rush Valley. It seems very unlikely *P. clarkii* is native, so far removed is Utah from its documented range. Introductions have resulted in established populations in California and Nevada (Pennak 1978), but any introductions of the species in this remote St. John site are undocumented and unexplained. Previous to its discovery, there was no reason to believe *P. clarkii* was present north of Lake Mead, Arizona-Nevada, and its tributaries.

Extensive fishery collections have been made in most of the Sevier River drainage and, based upon their absence from these collections, it seems reasonable to conclude crayfish are currently not in the drainage.

NEED FOR FURTHER STUDY

Because of the rapid expansion of *Orconectes virilis* in much of Utah, expansion of this species must be closely monitored and its impacts upon sportfisheries and native fauna should be documented. In addition to its potential impact on native crayfish, there are indications of negative effects of dense populations with rainbow trout recruitment and early growth (Hepworth and Duffield, in press), and near elimination of aquatic vegetation (Dean 1969). The effects of extensive removal of vegetation on invertebrate production and availability and diversity of littoral zone fishery habitats also require study.

The rash of surreptitious stockings of crayfish in recent years demonstrates an obvious need for a thorough public information program regarding the possible consequences of indiscriminate introductions. Such a program, to be most effective, requires basis in fact and would alone justify well-conceived research into crayfish population dynamics and ecosystem interactions.

Crayfish distribution is especially poorly documented in the western basins of Utah. Furthermore, the collection of *Pacifastacus leniusculus* in Utah County raises the question of whether that species is more widely distributed around Utah Lake or in the western basins. Any crayfish specimens from Utah County or the western basins would therefore be of particular interest.

ACKNOWLEDGMENTS

I am grateful to Dr. Horton H. Hobbs, Jr., U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C., for confirming the identity of specimens from my reference collection, for identifying *Procambarus clarkii*, and for his helpful comments. Specimens were collected by virtually every regional or research UDWR biologist. In addition, specimens and collection records from the Colorado River drainage were provided by V. Lamarra and R. Valdez of Ecosystem Research Institute, Logan, Utah; R. Radant, Nongame Section, UDWR, and H. Tyus, USFWS, Vernal, Utah.

This work was accomplished in conjunction with fishery studies funded by Federal Aid to Fish Restoration Projects F-43-R and F-44-R.

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CRYPTOGAMIC SOIL CRUSTS: RECOVERY FROM GRAZING NEAR CAMP FLOYD STATE PARK, UTAH, USA

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ABSTRACT.—The effects of grazing on the cryptogamic and vascular plant communities at two sites near Camp Floyd State Park, Utah County, Utah, were studied. The grazed site was subject to heavy grazing up until seven years prior to the study. The ungrazed site within the park boundaries had been protected from grazing for 20 years prior to the study and had a well-developed algal-lichen-moss crust. We found that the algae of the grazed site had recovered in terms of degree of crusting. There were no significant differences in the algal communities of the two sites when prevalent species were used as blocks in the ANOVAR analysis. However, when major algal groups were used as blocks, the analysis was significant, with the more recently grazed site having lower algal frequency. This difference, together with a few compositional differences, indicates that, although the algal community seven years following grazing is very similar to the algal community free of grazing for 20 years, the seven-year site is still in the process of recovery and community development. The diatom collections had a higher density in the grazed site, though the difference was not significant. Recovery of the lichen and moss community was not complete. The lichen *Collema tenax* and the mosses *Bryum pallescens* and *Tortula ruralis* were all significantly more abundant in the ungrazed area. Total cover of the lichen and moss components of the soil crusts was significantly lower in the more recently grazed area. Vascular cover was also lower.

Cryptogamic soil crusts are an important component of many arid rangeland ecosystems in the western United States. Such crusts have been found to be important in nitrogen fixation (Snyder and Wullstein 1973, Rychert and Skujins 1974) and enhancement of seedling establishment (St. Clair et al. 1984). The greatest benefit of cryptogamic crusts, however, is probably reduction of soil erosion. Soil aggregation, particularly by blue-green algae, reduces detachment of soil particles by wind and rain (Bailey et al. 1973, Anantani and Marathe 1974). Improved water penetration in crusted soils reduces runoff and subsequent erosion (Brotherson and Rushforth 1983). Sedimentation is also reduced by the increased tortuosity of surface water pathways due to the characteristic hummocking of desert crusts.

The effects of both burning and grazing on soil cryptogams have recently been investigated. Range fires can severely damage all components of the soil crust (Johansen, Javakul, and Rushforth 1982, Johansen et al. 1984, Callison et al. 1985). Several workers have noted that moderate to heavy grazing can seriously damage soil cryptogams because the crusts are trampled by livestock. Rogers and Lange (1971) noted that stocking pressure was negatively correlated with lichen cover and that soil mobility and erosion was increased in areas of reduced lichen cover. Kleiner and Harper (1972) found that the effects of grazing were more notable on the soil cryptogams than on the vascular plant communities in Canyonlands National Park. They also noted that soil erosion was higher in areas with lower cryptogam cover and observed changes in organic matter, available phosphorus, and calcium in eroded soils (Kleiner and Harper 1977). The effects of long-term moderate to heavy grazing near Navajo National Monument also showed that grazing has a more pronounced effect on the cryptogamic cover and diversity than on vascular plant cover and diversity (Brotherson et al. 1983). Burros in the Grand Canyon are currently causing erosion through destruction of *Tortula* (bryophyte) and lichen crusts (Phillips et al. 1977).

Several factors influence the development of cryptogamic crusts. Cryptogamic growth is best in soils of high electrical conductivity, high phosphorus, and high silt content (Anderson et al. *Factors*, 1982). Crust buildup is also positively correlated with soil alkalinity. The crusts of gypsiferous soils of southern

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Utah are particularly well developed, having high lichen and algal diversity (Anderson and Rushforth 1976). Recovery of crusts from disturbance follows several trends. Algae are the most resistant component to disturbance (Anderson et al. *Recovery*, 1982) and are also the quickest to recover (Johansen et al. 1984). Lichens and mosses are slower to recover. Anderson et al. *Recovery*, (1982) found that lichens and mosses had become fairly well established after a 14–17-year period of protection from grazing. Exclosures protected for 37–38 years showed little change in the moss flora, though lichen diversity was greater than in the 14–17-year-old exclosures. This paper also indicated a need for studies examining recovery in the first 15 years following protection from disturbance.

The primary purpose of our study was to determine the degree of recovery of the cryptogamic crust community in a soil that has been protected from grazing for seven years near Camp Floyd State Park. This study differs from past studies in that the grazed area is compared with an adjacent area that has been protected for 20 years rather than with an area still under grazing pressure.

SITE DESCRIPTION

The study was conducted near and within the boundaries of Camp Floyd State Park, Utah County, Utah. The park is located 0.4 km southwest of Fairfield, Utah, along State Highway 73 in central Utah and is relatively small (16.2 hectares). It was established in 1962 with the principal point of interest being an inactive military cemetery which occupies only a small portion of the total area of the park. The balance of the park has not been developed and is dominated by an *Atriplex confertifolia–Sarcobatus vermiculatus* desert shrub community. A well-developed cryptogamic soil crust flora consisting of various species of lichens, mosses, and algae is present. The soils at Camp Floyd belong to the Woodrow silt loam with an average water-holding capacity of 28–30 cm of water for the 1.5 m (5 ft) profile. This soil type has a slow permeability and is classified as a mixed (calcareous) mesic, xeric torifluvent. The mean annual rainfall in this area is 35 cm.

From 1935 until the establishment and subsequent fencing of the park area, the 1,600 hectares of shrubland immediately around the cemetery were heavily grazed by sheep and cattle during winter months (October to May). Fencing of the park property has effectively eliminated grazing in the park since 1962. This has permitted the establishment of a diverse and well-developed algal-lichen-moss community. The area outside the park continued to be heavily grazed until 1975, at which time livestock were removed from this range.

METHODS

Two permanent transects with points placed every 2 m were established in the vicinity of Camp Floyd State Park. The ungrazed area transect consisted of 6 points within the park boundaries. Data from this transect were compared with similar data collected from burned sites, and that comparison is the basis of a previous paper (Johansen et al., 1984). The grazed area transect consisted of 8 points one mile south of the park. Fieldwork was conducted from September to Novemeber, 1982.

Two crust samples were collected from each transect point at opposite compass points 0.25 m from the center of the point on 23 September 1982. Each sample was prepared for culturing by gently crushing soil clods to a maximum diameter of 5 mm. Twenty cm^3 of soil from each sample were placed in a sterilized petri dish and saturated with 20 ml of distilled water. Samples were then incubated under continous cool-white fluorescent light at room temperature (24 C) for 10 days. Percent visible algal cover in each petri dish was estimated at the end of the culture period. Frequency and relative abundance of living algal species were also estimated at that time by subsampling the center of each petri dish and examining this subsample under the light microscope. A total of 25 microscope fields were examined for each subsample, and presence and absence of each species in each field were noted. Permanent diatom mounts were prepared using standard acid oxidation procedures and Hyrax diatom mountant. Slides were prepared using quantitative dilutions for quantitative comparisons of soil diatoms (Johansen et al. 1982).

Visual estimates of total cryptogamic and vascular plant cover were made in the field

Table 1. Average percent frequencies of living algal species in grazed and ungrazed areas. Each species was tested using the Mann-Whitney test to determine if significant differences existed between treatments (* indicates $p<.05$, ** indicates $p<.01$). Estimated visible algal cover in culture dishes is also given.

Species	Grazed	Ungrazed
CYANOPHYTA		
Anabaena variabilis Kuetzing	.3	4.0
Aphanothece castagnei (Breb.) Rabh.	1.0	.3
Chroococcus minor (Kuetz.) Naegeli	1.0	.3
Chroococcus turgidus (Kuetz.) Naegeli		2.0
Gloeothece linearis var. *composita* G. M. Smith		.3
Microcoleus vaginatus (Vauch.) Gomont	55.0	57.0
Nostoc commune Vaucher	.5	10.0 *
Nostoc muscorum C. A. Agardh	.3	
Nostoc cf. *paludosum* Kuetzing	.8	1.7
Nostoc species	5.5	7.7
Phormidium minnesotense (Tild.) Drouet	27.8	15.3
Synechococcus aeruginosus Naegeli	.3	
Tolypothrix tenuis (Kuetz.) Schmidt	1.8	3.7
Unknown Chroococcaceae	1.5	4.0
CHLOROPHYTA		
Ulothrix tenerrima Kuetzing	.3	3.0
Unknown coccoids	16.3	23.0
BACILLARIOPHYTA		
Hantzschia amphioxys (Ehr.) Grunow	18.5	26.0
Navicula mutica Kuetzing	5.0	12.3
Navicula paramutica Bock	1.0	.3
Pinnularia borealis Ehr.	.8	.7
FLAGELLATES	.3	1.7
TOTAL SUM FREQUENCY	137.0	173.3
VISIBLE ALGAL COVER	16.6	36.5 **
SHANNON-WIENER DIVERSITY INDEX	2.35	2.75**

using a 1/4 m^2 circular quadrat placed at each permanent transect point. In addition to the 1/4 m^2 circular quadrats, a smaller 2 × 50 cm rectangular quadrat consisting of ten 2 × 5 cm subquadrats was placed perpendicular to the transect at each point and percent cover of algal crust and lichen and moss species was estimated. Cover was measured in November in the ungrazed area and in September in the more recently grazed area.

Soils were analyzed by the Soil Analysis Laboratory, Department of Agronomy and Horticulture, Brigham Young University, for pH, phosphorus, nitrate, Kjeldahl nitrogen, potassium, calcium, magnesium, zinc, iron, manganese, sodium, copper, organic matter, electrical conductivity, and sodium adsorption ratio. All samples were taken from the top 17.5 cm of soil for these analyses.

Mann-Whitney tests (Ryan et al. 1976) were performed for each species to determine significance levels of differences between grazed and ungrazed areas. This test was used in preference to the Students t-test (Snedecor and Cochran 1980) because some of our data were not normal. Shannon-Wiener diversity indices were calculated for the living algae and diatom communities for each transect point (Patten 1962, Shannon and Weaver 1949). Similarity indices for all 14 stands were calculated following the methods of Ruzicka (1958). Four different sets of similarity indices were calculated using lichen and moss cover, living algal density, diatom density, and vascular plant cover. These four sets of indices were then clustered following Sneath and Sokal (1973) to illustrate the degree of similarity between grazed and ungrazed stands in the four different plant communities. Importance values for species of living algae and diatoms were determined by multiplying average percent relative density times presence (Warner and Harper 1972). Species with importance values above 1.00 were used in the subsequent ANOVAR analyses.

Multivariate analysis of variance adapted in preference to the Students t-test (Snedecor for a fixed effects, unbalanced design following the methods of Bryce et al. (1980) was used to analyze differences between blocks (lichens mosses, algae, vascular plants) and treatments (time since grazing). Several separate ANOVAR tests were run, including tests using the vascular plant cover data, lichen and moss cover data, living algal data, and subfossil diatom data. In some data sets the variance of each species and group was related to the mean. To satisfy the homogeneity of variance assumption of analysis of variance for these data sets, a log (x+1) transformation was used (Bartlett 1947). With each analysis of variance, the standardized residuals were plotted against the normal scores to give a measure of normality. In all cases the probability plot thus generated was subjectively judged as being normal or close to normal. Our use of transects satisfied the requirements of systematic sampling as described by Cochran (1977). The Duncan multiple range test was used to determine significance of differences between species means when analysis of variance showed significance for this factor (Duncan 1955). Unless otherwise stated, the alpha level used for this test was 0.01.

RESULTS

Living Algae

The seven most important living algal species were *Microcoleus vaginatus* (importance value=55.86), *Phormidium minnesotense* (20.83), unknown green coccoid (18.46), *Hantzschia amphioxys* (17.06), *Nostoc* species (4.59), *Navicula mutica* (4.07), and *Nostoc commune* (1.42). Average percent frequencies for all algal species are given in Table 1. Multivariate analysis of variance based on the above seven prevalent species showed that the algal communities of the two areas were not significantly different. The Mann-Whitney test on the visual algal cover estimated in the field supported this conclusion (Table 3). The multivariate analysis did show that the species had significantly different frequencies. Duncan's test showed that *Microcoleus vaginatus* was significantly more abundant than all other algal species. *Phormidium minnesotense*, unknown coccoid green algae, and *Hantzschia amphioxys* were significantly more abundant than all less common algal species. The interaction between treatment and species was significant (p=.023). This was likely due to the fact that *Hantzschia amphioxys, Navicula mutica, Nostoc commune*, and coccoid green algae were all more abundant in the park area, whereas *Phormidium minnesotense* was more numerous in the more recently grazed stands (Fig. 1). *Microcoleus vaginatus* and *Nostoc* species showed only minor differences in frequency between the two sites.

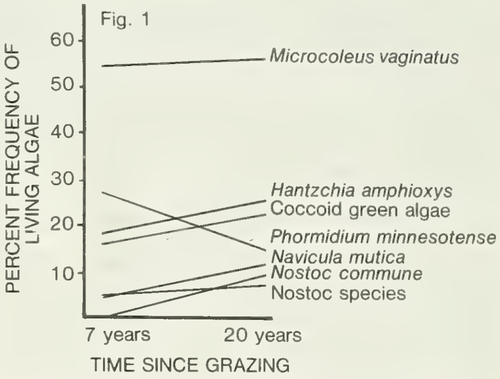


Fig. 1. Interaction between living algal species and treatment, significant at p=.023, using multivariate analysis of variance.

A separate analysis of variance was conducted to compare major algal groups. When using this data set, the difference between treatments was significant (p=.041), the more recently grazed plots having lower values. The groups were also significantly different (p<.001). Duncan's test showed that Cyanophyta were significantly more abundant than the other three algal groups. Bacillariophyceae and Chlorophyta were significantly more abundant than unidentified flagellates.

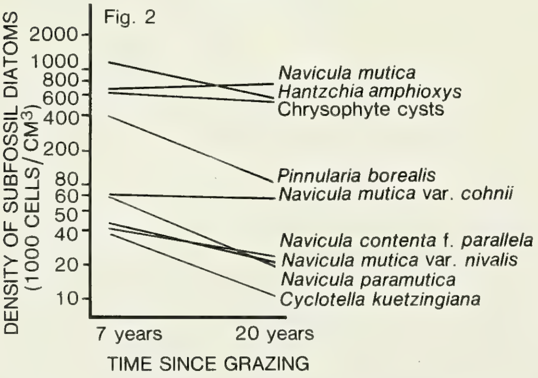
Nostoc commune had a significantly greater population in the 20-years-since-grazing area (p=.024) according to the Mann-Whitney test. No other living algal species or groups were significantly different at the two sites according to this test.

Subfossil Diatoms

The nine most important subfossil diatom species, including chrysophyte cysts observed in diatom mounts, were *Hantzschia amphioxys* (importance value 69.93), *Navicula mutica* (54.96), chrysophyte cysts (46.43), *Pinnularia borealis* (18.91), *Navicula mutica* var. *cohnii* (6.06), *Navicula paramutica* (3.65), *Navicula mutica* var. *nivalis* (2.42), *Navicula contenta* f. *parallela* (2.39), and *Cy-*

TABLE 2. Average densities (1,000 cells/cm) of diatom species in grazed and ungrazed areas. Each species was tested using the Mann-Whitney test to determine if significant differences existed between treatments (* indicates p<.05, ** indicates p<.01). Density of chrysophyte cysts is also given.

Species	Grazed	Ungrazed
Achanthes lanceolata Breb.	1	
Anomoeneis species	1	
Cocconeis placentula var. *lineata* (Ehr.) Cleve	5	1
Cyclotella kutzingiana Thwaites	39	11*
Denticula elegana f. *valida* Pedic.	2	1
Diploneis oblongella (Naeg. *ex* Kuetz.) Ross	1	
Epithemia adnata var. *minor* (P. & H.) Patr.		2
Epithemia turgida (Ehr.) Kuetzing	10	1**
Fragilaria brevistriata Grunow	3	
Fragilaria construens var. *venter* (Ehr.) Grunow	9	4
Fragilaria pinnata Ehr.		3
Hantzschia amphioxys (Ehr.) Grunow	1,250	562**
Melosira dendroteres (Ehr.) Ross		2
Melosira granulata (Ehr.) Ralfs	3	2
Melosira species	2	
Navicula contenta f. *parallela* Petersen	43	24
Navicula cuspidata (Kuetz.) Kuetzing	1	
Navicula elginensis var. *rostrata* (Mayer) Patr.		1
Navicula excelsa Krasske	3	2
Navicula mutica Kuetzing	698	728
Navicula mutica var. *cohnii* (Hilse) Grunow	85	78
Navicula mutica var. *nivalis* (Ehr.) Hust.	46	21
Navicula paramutica Bock	82	19**
Nitzschia paleacea		1
Pinnularia appendiculata (Ag.) Cleve		1
Pinnularia borealis Ehr.	404	105**
Pinnularia species	1	
Rhopalodia gibba (Ehr.) Mueller		1
Rhopalodia gibberula (Ehr.) Mueller		3
Stephanodiscus carconensis (Eul.) Grunow	1	
Stephanodiscus hantzschii Grunow	1	
Stephanodiscus species		2
TOTAL DIATOMS	2,690	1,570
TOTAL CHRYSOPHYTE CYSTS	675	530
SHANNON-WIENER DIVERSITY INDEX	1.94	2.14*



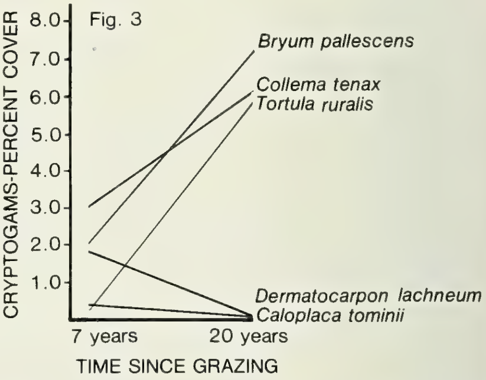


Fig. 2. Interaction between subfossil diatoms and treatment, significant at p<.001, using multivariate analysis of variance.

Fig. 3. Interaction between cryptogam species and treatment, significant at p<.001, using multivariate analysis of variance.

TABLE 3. Average percent cover values in grazed and ungrazed areas. Each species and cover class was tested using the Mann-Whitney test to determine if significant differences existed between treatments (* indicates $p<.05$, ** indicates $p<.01$).

Species	Grazed	Ungrazed
Cover based on 100 cm^2 rectangular quadrats		
LICHENS		
Caloplaca tominii Sav.	.4	.1**
Collema tenax (Sw.) Ach.	3.0	6.2**
Dermatocarpon lachneum (Ach.) A. L. Sm.	1.8	.1**
Lecidea decipiens (Hedw.) Ach.	—	P
TOTAL LICHEN COVER	5.1	6.4
MOSSES		
Bryum pallescens Schwaeg.	2.0	7.3**
Pterygoneurum lamellatum (Lindb.) Jur.		P
Tortula ruralis (Hedw.) Gaertn., Meyer & Scherb.	.3	6.1**
TOTAL MOSS COVER	2.3	13.4**
TOTAL ALGAL COVER	21.0	22.6
TOTAL CRYPTOGAMIC CRUST COVER	28.4	42.4

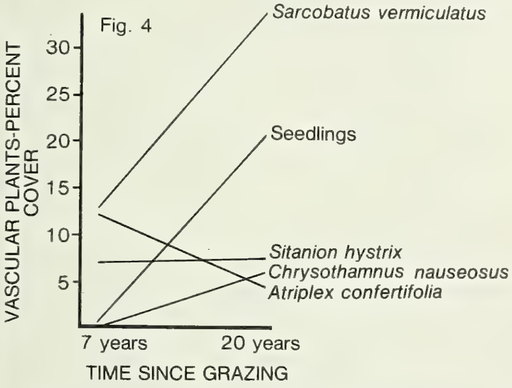


Fig. 4. Interaction between vascular plant species and treatment, significant at $p=.001$, using multivariate analysis of variance.

clotella kuetzingiana (1.52). Average densities of all diatom species are given in Table 2. Multivariate analysis based on the data for these nine taxa showed that diatoms were significantly more abundant in the recently grazed area ($p<.001$). Species were also significantly ($p<.001$) different. According to Duncan's test, *Hantzschia amphioxys*, *Navicula mutica*, and chrysophyte cysts were all significantly higher than the other diatom taxa. *Pinnularia borealis* was significantly more abundant than all less abundant species. *Navicula mutica* var. *cohnii* was more abundant than the other three prevalent species used in the analysis. The interaction between species and treatment ($p<.001$) is illustrated in Figure 2.

Lichens and Mosses

Multivariate analyses demonstrated several important differences among treatments, blocks, and interactions in the lichen and moss communities. Total lichen and moss cover was substantially greater in the park area ($p<.001$). Species of cryptogams had significantly ($p<.001$) different cover. Duncan's test showed that *Collema tenax* and *Bryum pallescens* were significantly more abundant than the other taxa. *Tortula ruralis* cover was significantly greater than *Caloplaca tominii* cover. The interaction between species and treatment was significant ($p<.001$). This was due to the fact the *Bryum pallescens*, *Tortula ruralis*, and *Collema tenax* had higher cover in the park area, whereas *Caloplaca tominii* and *Dermatocarpon lachneum* were most abundant in the more recently grazed area (Fig. 3).

A separate analysis of variance was run using total lichen and moss cover data. This test also showed a significant difference between treatment means ($p<.001$). The interaction between cryptogam class and treatment was significant ($p<.001$) because lichen cover is only slightly greater in the park area and moss cover is markedly greater in the park area. The Mann-Whitney test supports this conclusion in that the difference in total moss cover between treatments is significant, but the difference between mean lichen cover is not (Table 3).

TABLE 4. Average percent cover values in grazed and ungrazed areas. Each species and cover type was tested using the Mann-Whitney test to determine if significant differences existed between treatments (* indicates p<.05, ** indicates p<.01).

Cover type	Grazed	Ungrazed
Cover based on 1/4 m^2 circular quadrats		
Bare ground	21.1	4.3*
Litter	26.9	23.3
Cryptogamic crust	28.1	38.3
Total vascular plant cover	32.3	73.2
Atriplex confertifolia (Torr. & Frem.) S. Wats.	12.1	4.3
Chrysothamnus nauseosus (Pall.) Britt.		6.0
Sarcobatus vermiculatus (Hook.) Torrey	12.8	34.2
Sitanion hystrix (Nutt.) J. G. Smith	7.1	7.8
Vascular seedlings	.3	20.8**

TABLE 5. Average nutrient levels and soil characteristics of soil samples taken from grazed and ungrazed areas. Each factor was tested using a two-tailed t-test to determine if significant differences existed between treatments (* indicates p<.05).

Soil factor	Grazed	Ungrazed
pH	7.98	7.67
Phosphorus (ppm)	20.8	20.2
Nitrate-N (ppm)	6.03	6.30
Potassium (ppm)	944	743*
Calcium (ppm)	56.2	72.8
Magnesium (ppm)	8.4	13.5
Copper (ppm)	1.14	1.15
Zinc (ppm)	0.68	0.79*
Iron (ppm)	2.03	2.94*
Manganese (ppm)	2.34	3.33*
Sodium (ppm)	66	209*
Total organic matter (%)	1.30	1.71
Total nitrogen (%)	0.100	0.107
Electrical conductivity × 1000	0.91	1.81
Sodium adsorption ratio	0.41	1.54*

Multivariate analysis of the vascular plant community data showed that cover was significantly greater in the area protected from grazing for 20 years (p<.001). Species were also significantly different (p=.006), though only the means for *Sarcobatus vermiculatus* and *Chrysothamnus nauseosus* were significantly different according to Duncan's test. The interaction between treatment and species was also significant (p=.001) and is illustrated in Figure 4. Average percent cover values for all vascular species are given in Table 4.

The soils of the two sites were similar to each other (Table 5) though cations were generally higher in the park area. Students t-tests showed that the sites were significantly different in ppm K, Zn, Fe, Mn, Na, and sodium adsorption ratio. Except for potassium, the ungrazed site had greater values for all the above.

DISCUSSION

It is apparent from the data that the algal community, in terms of both the living algae and subfossil diatoms, has nearly recovered from the influence of grazing in the more recently grazed area. Visual estimates in the field as well as microscopic examinations in the laboratory support this conclusion. When the similarity indices for the transect points were clustered, all points were similar in regard to both living algae and subfossil diatoms. The greater density of subfossil diatoms in the more recently grazed area is difficult to explain. It may be due to the lower vascular plant density in the grazed area, which in turn results in increased light intensity and lower litter cover. These factors in combination could favor diatom growth.

The dominant lichen and moss species of this area, *Collema tenax*, *Bryum pallescens*, and *Tortula ruralis*, have not fully recovered in the grazed area. An unusual observation was the significantly greater amount of the lichen *Dermatocarpon lachneum* in the more recently grazed area. We hypothesize that this may indicate an intermediate successional stage in the recovery process. Factors contributing to this phenomenon may include compositional differences in both the vascular and nonvascular plant communities as well as biological modifications of local abiotic factors such as light and moisture. This hypothesis will be tested by future monitoring of the lichen and moss community at these two sites.

The greater density of the three dominant lichen and moss taxa in the ungrazed area

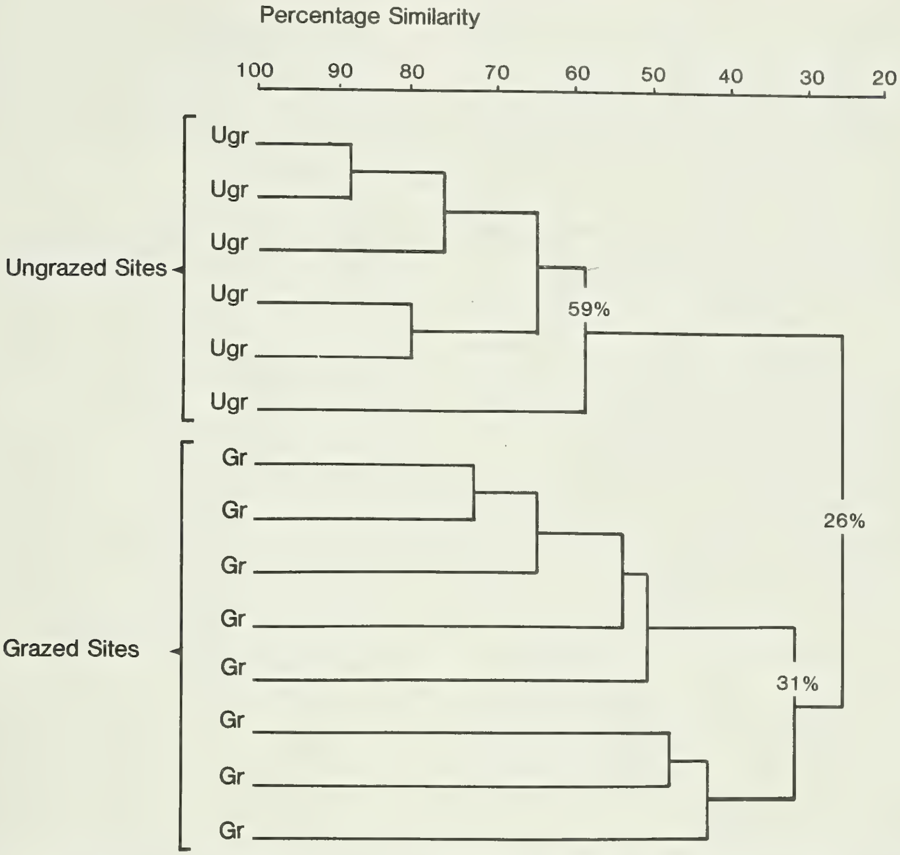


Fig. 5. Fourteen transect points clustered on the basis of Ruzicka's similarity index as computed from lichen and moss data. All stands were similar, yet still clustered into two main groups, i.e., grazed and ungrazed sites.

combined with the significantly greater cover of *D. lachneum* in the more recently grazed area resulted in the formation of discrete site groupings when similarity indices of transect points were clustered (Fig. 5). However, the two clusters based on algal data did not form such discrete clusters, probably because of the high level of similarity between all points. This demonstrates that the algal community has essentially recovered in the seven years following removal of livestock from the range, whereas the lichen and moss communities are still in the process of recovery.

Anderson et al. *Recovery*, (1982) indicate that reestablishment of cryptogamic soil crusts is substantial after 14–18 years. Our study indicates that the recovery rate of the algae is much more rapid than estimated in their study, occurring in fewer than 7 years. The lichens and mosses, on the other hand, fit the predicted recovery patterns and apparently require more than 7 years to fully recover.

An important dimension in the development of soil crusts is frequency and abundance of moisture. The annual precipitation in Utah County has been above normal for the past three years and has undoubtedly played a role in the reestablishment of the soil crusts at the disturbed sites near Camp Floyd. Subjective observations of the grazed site in 1981 indicated that differences between visible cryptogamic cover were evident. Noticeable recovery of the crust in the grazed area occurred during the ensuing moist year before the present study was undertaken. It is possible that in drier areas or drier years development of cryptogamic crusts following grazing disturbance might take longer than the seven-year period observed in the present study.

The greater cover of vascular seedlings observed in the ungrazed area was likely due to temporal differences in sampling. The more recently grazed area was examined in September, whereas the ungrazed area was sampled in November after two months of mild, moist weather. A noteworthy difference in vascular plant community structure was observed. *Atriplex confertifolia* populations were substantially greater in the grazed area (Fig. 4). On the other hand, *Sarcobatus vermiculatus* was most dense in the ungrazed area. Sheep have been known to browse both *Sarcobatus* and *Atriplex*. Thus, over a period of 40 years the abundance of both taxa could have been severely reduced in the grazed area. With the end of grazing pressure, *Sarcobatus vermiculatus*, a vigorous root sprouter, has begun reestablishing itself. In the area protected for 20 years, the development of the *Sarcobatus* population has possibly proceeded to the point that *Atriplex* is being crowded out. In the more recently grazed area the vascular cover is less abundant, and *Atriplex* has not been excluded.

ACKNOWLEDGMENTS

This research was supported by the Shrub Sciences Laboratory, Forest Service, USDA, Provo, Utah 84601. Dr. Brent Mishler of Duke University kindly assisted in identifying our bryophyte material.

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NEW SPECIES AND NEW RECORDS OF NORTH AMERICAN *PITYOPHTHORUS* (COLEOPTERA: SCOLYTIDAE), PART VI. THE LAUTUS GROUP

Donald E. Bright[1]

Abstract.—Four new species of Mexican *Pityophthorus* in the Lautus group are described: *P. indefessus* (Jalisco), *P. inhabilis* (Guerrero), *P. tutulus* (Veracruz), and *P. vegrandis* (Quintana Roo) and a new locality record is given for *P. corruptus* Wood.

This is the third paper describing the previously unnamed species of *Pityophthorus* collected by Dr. T. H. Atkinson and his colleagues (Centro de Entomología y Acarología, Colegio de Postgradados, Chapingo, Mexico). The present contribution describes four species in the Lautus group and gives new locality records for one species in the group. As in the previous papers (Great Basin Nat. 45: 467–482), the key in my 1981 monograph (Mem. Ent. Soc. Canada 118, pp. 54, 55) is modified to accommodate the newly named species.

I thank Dr. Atkinson for sending the specimens to me and also thank him and his students for their diligent searching for Scolytidae in previously unrecognized host plants. I also thank my colleagues Dr. Y. Bousquet and Dr. L. LeSage for reviewing the manuscript.

Pityophthorus indefessus, n.sp.

Length 1.3–1.4 mm, 2.7 times longer than wide.

Frons transversely impressed from epistomal margin to upper eye level, impression moderately deep, with obscure, weakly elevated, impunctate median carina extending from epistoma halfway or less across impression; surface shining, finely, densely punctured, setae short, inconspicuous. Antennal club 1.1 times longer than wide, widest through third segment; first two sutures weakly arcuate, almost invisible except where heavily sclerotized at lateral margins; first two segments occupy about one-third of total club length. Pronotum slightly more than 1.1 times longer than wide, widest at level of summit; sides very weakly arcuate, weakly converging on posterior half, broadly rounded anteriorly, anterior margin with about nine distinct serrations; anterior slope with three irregular rows of asperities, these rows somewhat broken, several obscure additional rows around summit; summit weakly elevated; posterior area of disc with numerous fine, shallow punctures, these separated by distance equal to or less than their diameters, surface between punctures shining, smooth with numerous, very fine impressed points; median line obscure, narrow, impunctate. Elytra 1.6 times longer than wide, apex very broadly rounded, almost truncate; discal striae punctured in regular rows, punctures fine, shallow, slightly larger than those on posterior portion of pronotum; interstriae about twice as wide as striae, moderately shining, with numerous, very fine, minute points, 3, 5, 7 with three or four erect, flattened scales on posterior half, 1 with row of four or five scales extending to base. Declivity convex, flattened; interstriae 1 elevated, with median row of fine granules and short, fine setae; interstriae 2 weakly impressed, with median row of very fine setae and granules, these sometimes evident only on upper half of interstria; interstriae 3 very weakly elevated, with median row of distinct, fine granules and erect, spatulate setae, these longer than setae on 1 and 2; remaining interstriae (3, 5, 7) with a median row of erect spatulate setae; punctures in striae 1 and 2 distinct.

Type material.—The holotype is labeled: "Estación Biológica, Chamela, Edo. Jalisco, 7.III.82, S-390, 80 msnm, Col. Armando Equihua"/"HOLOTYPE Pityophthorus indefessus D. E. Bright, 1986, CNC 18747." Two paratypes bear the same locality data plus paratype labels. The holotype is in the Canadian National Collection; the two paratypes were returned to T. H. Atkinson.

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COMMENTS.—The sexes of the three specimens in the type series could not be determined since, in this group, sex can only be estabilished by examining the abdominal tergites. This was not done on the three specimens at hand.

The specimens in the type series were found in a sample of *P. molestus* Wood and are very similar to that species except that declivital interstria 2 of *P. indefessus* bears a row of fine granules and very fine setae, these present or most obvious on upper half of the interstria. This species will key to near *P. nemoralis* Wood and *P. concentralis* but may be distinguished by the characters mentioned in the key.

Pityophthorus inhabilis, n.sp.

Length 1.8–2.0 mm, 3.0 times longer than wide.

FEMALE.—Frons flattened on semicircular area extending laterally from eye to eye and longitudinally from epistoma to well above upper eye level; surface densely, closely punctured in flattened area with brush of dense, erect setae all of equal or nearly equal length, surface above and lateral to flattened area shining, glabrous, with much larger, deeper, sparser punctures. Antennal club oval, about 1.4 times longer than wide, widest through second segment; suture 1 transverse, heavily sclerotized except for short space in middle, 2 transverse, lightly sclerotized only at lateral margin; segments 1 and 2 occupy more than two-thirds of total club length, suture 1 located just below middle of club, 2 located just below apex of club. Pronotum 1.1 times longer than wide, widest at posterior angles; sides slightly converging to broadly rounded anterior margin; asperities on anterior slope arranged into 4–6 or more irregular concentric rows, first row more regular, remaining rows slightly broken; summit distinct; posterior area of disc moderately shining, punctures large, deep, close, interpuncture space with numerous, fine, impressed points; median line narrow, not elevated, impunctate. Elytra 1.8 times longer than wide; apex narrowly rounded, elevated interstriae 1 extending slightly beyond elytral outline; discal striae punctured in regular rows, punctures large, larger than those on posterior portion of pronotum, deeply impressed; discal interstriae about as wide as or narrower than striae, moderately shining, glabrous, with numerous, fine, impressed points. Declivity almost evenly convex, weakly bisulcate; interstriae 1 wide, distinctly elevated, with median row of fine, shallow punctures and short, fine setae; interstriae 2 weakly impressed, flat, glabrous, slightly wider than strial width; interstriae 3 very weakly elevated, with several, large punctures and short, fine setae; striae 1 narrowly impressed, punctures obscure, 2 distinctly punctured, slightly curved in middle; vestiture in remaining interstriae consisting of fine setae near declivity.

MALE.—Frons weakly transversely impressed to upper level of eyes; surface of impressed area densely, coarsely punctured, setae absent except along epistomal margin, surface above and lateral to impression more deeply, less closely punctured. Antennal club with first suture slightly closer to base than on female, second suture very weakly indicated near apex. Pronotum and elytra essentially as described for female. Declivity slightly more deeply bisulcate, otherwise as described for female.

TYPE MATERIAL.—The holotype (♀) is labeled: "Chilapa, Guerrero, 23-II-82, 1800 m, S-337, Col. Atkinson y Equihua"/"HOLOTYPE Pityophthorus inhabilis D. E. Bright, 1986, CNC No. 18447." The allotype and six paratypes bear the same locality label plus the appropriate type label.

The holotype, allotype, and two paratypes are in the Canadian National Collection; four paratypes were returned to Dr. Atkinson.

COMMENTS.—Compared to adults of other species in the Lautus group, those of this species are unique by having a more broadly sloping elytral declivity on which the first and second striae are distinct, by having distinct sexual dimorphism on the frons, and by the unique antennal club on which the first two segments occupy almost the entire face of the club. The first antennal suture is located near the middle of the club and is distinctly sclerotized; the second suture is located just before the apex of the club and is weakly sclerotized and obscure. Other characters of species in the Lautus group, such as the concentric rows of pronotal asperities and the distinctly punctured first and second declivital striae, are all present on adults of this species.

Pityophthorus tutulus, n.sp.

Length 1.5–1.8 mm, 2.8 times longer than wide.

FEMALE.—Frons broadly flattened to weakly concave from eye to eye and from epistoma to well above eyes; surface on lower half smooth, moderately shining, sometimes with few, minute, impressed points and few, scattered setae, upper half with dense covering of very short, stout, recumbent scales, periphery of flattened area with row extending from eye to eye of long, incurved setae. Antennal club large, elongate-oval, 1.5 times longer than wide, widest through segment 3; suture 1 weakly arcuate, 2 transverse, both sclerotized, 2 more so than 1; segments 1 and 2 together occupy about one-third of total club length. Pronotum 1.1 times longer than wide, widest at middle; sides weakly arcuate, feebly constricted before broadly rounded anterior margin; asperities on anterior slope arranged into three distinct and one or two indistinct concentric rows; these rows may be broken, especially in median area; summit distinct; posterior area of disc moderately shining, punctures of moderate size, deep, distinct, close, interpuncture space with numerous, distinct, minute, impressed points; median line broad, not elevated, with numerous impressed points. Elytra 1.6 times longer than wide; apex broadly rounded; discal striae punctured in regular rows, punctures large, larger than those on posterior portion of pronotum, deeply impressed, close; discal interstriae about as wide or slightly narrower than striae, surface moderately shining, glabrous, with numerous fine points and lines. Declivity steep, convex; interstriae 1 very slightly impressed below level of 3 on upper half, with median row of fine granules; interstriae 2 flat, as wide as on disc, weakly but distinctly impressed below 1, surface smooth, glabrous; interstriae 3 weakly elevated, with median row of fine granules; striae 1 narrow, distinctly impressed, 2 slightly less deeply impressed, both straight and distinct; vestiture consisting of fine setae on lateral interstriae and in all interstriae, except 2, near declivity.

MALE.—Frons weakly concave, upper margin of concavity arcuate, extending above upper level of eyes; surface minutely punctate, with few, scattered, fine setae. Otherwise essentially as in female.

TYPE MATERIAL.—The holotype (♀) is labeled: "Jalapa, Veracruz, 28-XI-83, FANM 100, col. Felipe A. Noguera"/"Hosp. Rhus radicans (Anacardiaceae)"/"HOLOTYPE Pityophthorus tutulus D. E. Bright, 1986, CNC No. 18448." The allotype and six paratypes bear the same locality and host data plus the appropriate type labels.

The holotype, allotype, and two paratypes are in the Canadian National Collection; four paratypes were returned to Dr. Atkinson.

COMMENTS.—This species and *P. crinalis* are unique among North American species of the genus in that the upper half of the female frons has a dense brush of numerous short, recumbent, plumose scales. This brush extends from eye to eye and has a fringe of much longer, incurved plumose setae on the upper margin (see figure 37 in my 1981 monograph). The lower half of the female frons is smooth, shining, and glabrous. The males of these two species differ from those of other species in the group only in minor details. Both species occur in *Rhus* spp.

Adults of *P. tutulus* differ from those of *P. crinalis* by the slightly larger body size, by the larger antennal club, by the slightly larger granules on declivital interstriae 1 and 3, by the slightly more deeply impressed elytral declivity, and by the distribution.

Pityophthorus vegrandis, n.sp.

Length 1.0–1.1 mm, 2.7 times longer than wide.

FEMALE.—Frons evenly convex, very weakly transversely, narrowly flattened just above epistoma; surface dull, densely microreticulate, with very faint, shallow, scattered punctures, setae absent except along epistomal margin. Antennal club oval, 1.4 times longer than wide, widest through segment 3; suture 1 moderately arcuate, sclerotized through entire length, suture 2 transverse to weakly arcuate, sclerotized at lateral margins; segments 1 and 2 together occupy about one-half of total club length. Pronotum as long as wide, widest at level of summit; asperities on anterior slope arranged into three even concentric rows, one very faint additional row may be detected around summit; summit distinctly elevated; posterior area of disc smooth, dull, densely microreticulate, with large, shallow, widely separated punctures; median line broad, impunctate, reticulate. Elytra about 1.6 times longer than wide; apex broadly rounded; discal striae punctured in even rows, punctures fine, shallow, smaller than those on posterior portion of pronotum; interstriae about 1.5 times wider than striae, surface smooth or weakly reticulate, shining, without setae. Declivity convex, steep; interstriae 1 and 3 equal in height, both with median row of very fine granules; interstriae 2 flat, equal to discal width, weakly impressed below level of 1 and 3; striae 1 and 2 weakly impressed, 1 more strongly so; scattered setae present in all interstriae except 2.

MALE.—Virtually identical to female except frons very weakly flattened, with distinct, large, deeply impressed punctures.

TYPE MATERIAL.—The holotype (♀) is labeled: "Chetumal, Quintana Roo, 10-Julio-1982, 20 m, SM-020, E. Martinez"/"HOLOTYPE Pityophthorus vegrandis D. E. Bright, 1986, CNC No. 18449." The allotype and one paratype bear the same locality label plus the appropriate type label. One damaged specimen, not designated as a paratype, is labeled: "Laguna de Bacalar, Quintana Roo, 10-Julio-1982, 20 m, SM-020, E. Martinez."

The holotype and allotype are in the Canadian National Collection; the two paratypes were returned to Dr. Atkinson.

COMMENTS.—The relationships of this species are unclear. Although it keys to near *P. sambuci*, the two are not closely related. Adults are most easily distinguished by the small size, by the dull, densely, minutely reticulate frons of both sexes, by the very weakly impressed elytral declivity, and by the weak development of sexual dimorphism.

Revised key to species in the Lautus group

1. Male and female frons similar, pubescence sparse 2

— Male and female frons sexually dimorphic, female frons distinctly pubescent, male frons only sparsely pubescent 11

2(1). Declivital interstriae 2 bearing median row of fine punctures or fine setiferous granules and fine setae; antennal club narrowly oval, about 1.5 times longer than wide 3

— Declivital interstriae 2 never bearing granules or setae; antennal club broadly oval, less than 1.5 times longer than wide 5

3(2). Declivital interstriae 2 bearing a median row of fine setae, these as long as those on interstriae 1 and 3; surface between punctures on pronotum strongly reticulate; Honduras to Costa Rica .... *nemoralis* Wood

— Declivital interstriae 2 bearing a median row of fine granules or punctures and fine setae, setae much shorter than those on interstriae 3 (and sometimes 1); surface between punctures on pronotum smooth or with fine points, brightly shining 4

4(3). Declivital interstriae 2 bearing a median row of fine punctures and extremely fine hairlike setae; setae on declivital interstriae 3–9 all hairlike; surface between punctures on pronotum smooth; frons without longitudinal carina above epistoma; Florida and Cuba .... *concentralis* Eichhoff

— Declivital interstriae 2 bearing a median row, at least on upper half, of fine granules and fine, flattened setae; setae on declivital interstriae 3–9 spatulate; surface between punctures on pronotum with numerous fine points; frons with a weak longitudinal carina extending from epistoma halfway to upper eye level; Jalisco .... *indefessus* Bright

5(2). Frons bearing weak but distinct, longitudinal carina or elevation; punctures on posterior portion of pronotum numerous, small, and shallow (except *borrichiae*) 6

— Frons without indication of carina, sometimes bearing very small tooth on epistomal margin; punctures on posterior portion of pronotum large, deep, and widely spaced 10

6(5). Frons flattened or transversely concave to upper level of eyes, divided by weak, longitudinal, narrow elevation; declivity sloping; asperities on anterior pronotal slope arranged into broken concentric rows 7

— Frons convex, usually with distinct, narrow elevation extending from epistoma to vertex, elevation interrupted in center by weak, transverse impression; if elevation absent, then frons rugose, elevation frequently indicated by small, elongate callus at upper level of eyes; declivity steep; asperities on anterior pronotal slope arranged in even, concentric rows 8

7(6). Occurs in eastern United States; setae on declivital interstriae about 1.5 times longer than interstrial width; median elevation on frons only weakly indicated .... *lautus* Eichhoff

— Occurs in eastern Mexico; setae on declivital interstriae longer, more than 2.0 times longer than interstrial width; median elevation on frons sharply elevated .... *molestus* Wood

8(6). Body length 1.0–1.3 mm; declivital setae stout, about equal in length to interstrial width; Florida .... *borrichiae* Wood

— Body length 1.4–1.7 mm; declivital setae fine, hairlike, nearly 2.0 times longer than interstrial width; Mexico and Central America 9

9(8). Frons shining, deeply punctured, frontal elevation not evident but frequently indicated by elongate callus at upper level of eyes; discal interstriae smooth, with sparse, minute points; Chiapas to Honduras . . . *morosus* Wood

— Frons dull, reticulate, sparsely punctured, elevation usually distinct but frequently interrupted in middle by weak, transverse, densely punctured impression; discal interstriae with numerous fine lines, surface irregular; Mexico . . . . *patulus* Wood

10(5). Frons evenly convex or weakly flattened, surface dull, microreticulate; surface between punctures on posterior portion of pronotum densely reticulate; length 1.0 mm; Quintana Roo . . . . *vegrandis* Bright

— Frons flattened, usually with small tooth or weak elevation on epistomal margin, surface shining, smooth; surface between punctures on posterior portion of pronotum shining, smooth or faintly reticulate; length 1.4–1.7 mm; Jalisco . . . . *sambuchi* Blackman

11(1). Female frons densely pubescent only on upper margin above upper level of eyes, shining and glabrous below; male frons flattened, densely punctured 12

— Female frons pubescent over entire area between eyes, setae may be longer, more abundant on periphery of flattened area; male frons weakly transversely impressed 15

12(11). First two segments of antennal club occupy more than two-thirds of total club length; declivity very weakly bisulcate, interstriae 2 widened, flat; male frons weakly transversely impressed, setae sparse; female frons flattened with erect setae, all of equal length; Guerrero . . . . *inhabilis* Bright

— First two segments of antennal club occupy less than two-thirds of total club length; declivity variable, not as above; male frons variable; female frons variable, with setae in various patterns but not as above 13

13(12). First two segments of antennal club occupy more than half of total club length, club 1.4 times or less longer than wide; lower half of female frons weakly but distinctly punctured, punctures rather large, upper margin with fringe of plumose setae; southeastern USA . . . . *liquidambaris* Blackman

— First two segments of antennal club occupy about one-third of total club length, club 1.5 times longer than wide; lower half of female frons smooth, brightly shining, sometimes with minute punctures, upper area with dense recumbent scales in addition to setae . 14

14(13). Occurs in eastern USA; length 1.3–1.6 mm . . . . *crinalis* Blackman

— Occurs in southern Mexico; length 1.5–1.8 mm . . . . *tutulus* Bright

15(11). Occurs in Central America; setae on declivital interstriae scalelike in male, hairlike in female; pubescence on female frons abundant on periphery, sparse in central area . . . . *perexiguus* Wood

— Occurs in Mexico; setae on declivital interstriae as above or hairlike in both sexes; pubescence on female frons variable 16

16(15). Body size 0.8–1.6 mm; female frons pubescent on narrowly oval, median area, all setae of equal length; granules on declivital interstriae 3 large, setae on declivity scalelike in male, hairlike in female; Mexico . . . . *attenuatus* Blackman

— Body size 1.5–1.8 mm; female frons pubescent on broad area extending from eye to eye and to above upper eye level; central portion of female frons less densely pubescent, setae on periphery longer; granules on declivital interstriae 3 small; setae on declivity hairlike in both sexes . . . . . *corruptus* Wood

NEW RECORD

Pityophthorus corruputus Wood

Pityophthorus corruptus Wood, 1976, Great Basin Nat. 36, p. 363; Bright, 1981, Mem. Ent. Soc. Canada 118, p. 68; Wood, 1982, Mem. Great Basin Nat. 6, p. 1133.

This species was previously known only from the type series from Puebla. A series of 29 specimens were seen bearing the labels: "San Rafael, Mex., 4.IX.81, S-242, 2400 m, Atkinson - Equihua"/"Hosp.: *Rhus* sp."

The specimens are identical to the two paratypes in the Canadian National Collection.

INITIAL SURVEY OF ACETYLENE REDUCTION AND SELECTED MICROORGANISMS IN THE FECES OF 19 SPECIES OF MAMMALS

C. Y. Li[1], Chris Maser[2], and Harlan Fay[1]

ABSTRACT.—Nitrogen-fixing bacteria, as demonstrated by the acetylene reduction method; yeasts, and actinomycetes were found in feces of mammals collected from St. Lawrence Island, Alaska, to the North Carolina–Tennessee border. The mammals, representing four orders and 19 species, occupy a wide variety of habitats and may play an important role in dispersing microorganisms vital to the ecosystem.

The California red-backed vole (*Clethrionomys californicus*), the northern flying squirrel (*Glaucomys sabrinus*), and the deer mouse (*Peromyscus maniculatus*) are forest-dwelling rodents that may play an important role in maintaining forest productivity. These mammals consume hypogeous mycorrhizal fungi and disperse fecal pellets containing fungal spores, which germinate and form mycorrhizae with roots of forest trees (Hunt and Maser 1985, Maser et al. 1978; *Food habits*, 1985; *Northern flying squirrel*, 1985; Ure and Maser 1982). The feces of these animals also contain nitrogen-fixing bacteria and yeast. The nutrient in the feces is as effective as yeast extract in promoting bacterial growth and nitrogenase activity (Li et al. 1986). When these animals dig at the bases of trees, the organisms in their feces could inoculate rootlets with nitrogen-fixing bacteria, yeast, and spores of mycorrhizal fungi. At times, actinomycetes are also present; they produce substances important in formation of soil humus (Krassilnikov 1981).

Having worked out the basic links in the abilities of small mammals in western Oregon to pass viable nitrogen-fixing bacteria and yeast through their digestive tracts (Li et al. 1986), the next question was, How widespread is this phenomenon? We conducted a survey of feces of 51 mammals of 19 additional species, collected from St. Lawrence Island, Alaska, to the North Carolina–Tennessee border, for acetylene-reducing (nitrogen-fixing) bacteria (Postgate 1982), yeasts, and actinomycetes.

MATERIALS AND METHODS

Fresh fecal pellets from 51 mammals of 19 species, representing four orders, were collected in sterile vials (see Li and Maser 1986 for collecting techniques).

Acetylene Reduction Activity

One fecal pellet each from 48 small mammals was placed in 20 ml of Döbereiner's N-free liquid medium (Döbereiner and Day 1976) and Burk's (1930) liquid medium in a 60-ml serum bottle. We used only the central portions of the pellets from three large mammals: black-tailed jackrabbit (*Lepus californicus*), eastern cottontail (*Sylvilagus floridanus*), and elk (*Cervus elaphus*). Bottles were capped and flushed for 5 min with nitrogen gas containing less than 10 ppm oxygen. The liquid medium became turbid after incubation for two days at 30 C. Acetylene was then injected into each bottle to 10 percent (v/v); the bottles were gently swirled immediately after acetylene was added and were left to stand at 30 C. Bottles without acetylene injection served as controls. After 18 hr, 0.1 ml gaseous samples were removed from each bottle and analyzed for ethylene and acetylene with a Hewlett-Packard 5830A gas chromatograph[3] fitted with a 2 m × 2.1 mm, 80–100 mesh Poropak R column. Oven temperature was adjusted to 70 C. Injection and flame ionization detector temperatures were each adjusted to 100 C. Nitrogen carrier gas flow rate was adjusted to 40 ml/min.

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[3] Use of trade names does not imply endorsement or approval of any product by the USDA Forest Service to the exclusion of others that may be suitable.

TABLE 1. Nitrogenase activity and microorganisms in feces of 51 mammals of 19 species from Alaska to North Carolina–Tennessee.

Animal	Geographic location	Nitrogenase[1] activity	Yeasts[2]	Actinomycetes[2]
INSECTIVORA				
Soricidae (shrews)				
Sorex cinereus (1)[3]	Morocco, IN	+	not determined	not determined
LAGOMORPHA				
Leporidae (hares and rabbits)				
Lepus californicus (1)	Summer Lake, OR	+	+	+
Sylvilagus floridanus (1)	Morocco, IN	+	0	0
RODENTIA				
Sciuridae (squirrels)				
Cynomys leucurus (7)	Meeteetse, WY	0	+	0
Cynomys leucurus (3)	Laramie, WY	0	+	0
Eutamias townsendi (1)	Umpqua, OR	+	+	+
Glaucomys volans (2)	Morocco, IN	+	+	0
Spermophilus parryi (1)	St. Lawrence Island, AK	0	+	0
S. tridecemlineatus (2)	Cedar Falls, IA	+	+	+
Tamias striatus (1)	Cedar Falls, IA	+	+	+
Geomyidae (pocket gophers)				
Geomys busarius (1)	Morocco, IN	+	0	+
Cricetidae (native mice)				
Peromyscus leucopus (6)	Morocco, IN	+	+	0
P. maniculatus (4)	Morocco, IN	+	0	0
Arvicolidae (voles)				
Clethrionomys gapperi (10)	Roon Mountain, NC–TN	+	+	+
Lagurus curtatus (1)	Silver Lake, OR	+	+	+
Microtus ochrogaster (2)	Morocco, IN	+	+	0
M. oeconomus (4)	St. Lawrence Island, AK	+	+	0
M. oregoni (1)	Marys Peak, OR	+	+	+
Muridae (Old World mice)				
Mus musculus (1)	Morocco, IN	+	+	+
ARTIODACTYLA				
Cervidae (deer)				
Cervus elaphus (1)	Post, OR	0	+	0

[1] Four replicates (all positive or all negative).
[2] Average of three replications of one individual from each species.
[3] Number of individuals tested for nitrogenase activity.

Bacterial cultures that reduced acetylene were all isolated but were not all purified.

Yeast and Actinomycetes

Sodium albumenate agar (Waksman and Fred 1922) was used to test for yeast and actinomycete populations. One fecal pellet (or central portion of a pellet from the three large mammals) per vial was removed with sterile forceps under an isolation hood. Each pellet was crushed and thoroughly mixed in 30 ml of sterile distilled water. One ml, 0.5 ml, and 0.1 ml of this fecal suspension were each plated with 20 ml of sodium albumenate agar. Colonies developed on the surface of the agar. The presence of yeasts and actinomycetes was confirmed under a light microscope, and colonies were counted after three days' incubation at 30 C. Colonies were sometimes so numerous, even at high dilutions, that their numbers had to be estimated.

RESULTS AND DISCUSSION

Results of our study are given in Table 1.

Acetylene Reduction Activity

Feces of mammals of the 19 species were tested for acetylene reduction, which is a universal and specific property of nitrogenase of nitrogen-fixing bacteria (Postgate 1982). Sixteen samples were positive (Table 1). Thirteen of the 19 species are known to eat the fruiting bodies of hypogeous, mycorrhizal fungi from which they could ingest nitrogen-fixing bacteria (Li and Castellano 1985, 1986). These 13 mycophagists are: masked shrew (*Sorex cinereus*) (Hamilton 1941); *Lepus cali-*

fornicus (Ponder 1980); Townsend chipmunk (*Eutamias townsendi*) (Maser et al. 1978); southern flying squirrel (*Glaucomys volans*) (Maser and Maser, unpublished data); eastern chipmunk (*Tamias striatus*) (Maser and Maser, unpublished data); white-footed mouse (*Peromyscus leucopus*) (Fogel and Trappe 1978, Maser et al. 1978, Whitaker 1966); *P. maniculatus* (Hunt and Maser 1985, Maser et al. 1978); southern red-backed vole (*Clethrionomys gapperi*) (Fogel and Trappe 1978, Maser et al. 1978, Ure and Maser 1982); sage vole (*Lagurus curtatus*) (Dowding 1955, Maser et al. 1978); prairie vole (*Microtus ochrogastar*) (Fogel and Trappe 1978); tundra vole (*M. eoconomus*) (Fogel and Trappe 1978); creeping vole (*M. oregoni*) (Maser et al. 1978); and house mouse (*Mus musculus*) (Whitaker 1966).

Yeast

Mammals that feed on fungi can also ingest yeasts (Anderson and Skinner 1947, Kockova-Kratochvilova et al. 1984). Yeasts were virtually ubiquitous in our samples and passed through the digestive tracts of 15 of the 18 species checked (Table 1). Yeast propagules ranged from zero to an estimated 1,800,000 per pellet.

Actinomycetes

Actinomycetes, often called "ray fungi," are actually higher bacteria. They may occur both in soil and on the surfaces of plant leaves (Dickinson et al. 1975, Lechevalier 1981). Of the 18 species examined for actinomycetes, the 9 that were positive (Table 1) are known to eat substantial amounts of green vegetation (Bailey 1936, Bee and Hall 1956, Hamilton and Whitaker 1979, Hansen and Flinders 1969, Lechleitner 1969, Whitaker 1966). Actinomycetes ranged from zero to an estimated 600,000 per fecal pellet.

Potential Interrelations

Mammals generally are abundant and mobile and form functional links with all areas of the terrestrial habitat, from below the ground into the tree tops. They deposit fecal pellets throughout their habitats. Fecal pellets of some species contain viable nitrogen-fixing bacteria, yeast propagules, and actinomycetes (Table 1). Yeast and actinomycetes apparently can be obtained by mammals on plant material (Dickinson et al. 1975, Lechevalier 1981); however, nitrogen-fixing bacteria in pellets seem to be associated more with soil and food obtained below the ground. For example, feces of white-tailed prairie dog (*Cynomys leucurus*), arctic ground squirrel (*Spermophilus parryi*), and *Cervus elaphus* showed no acetylene reduction activity (Table 1); their sole diet in early summer when the pellets were collected might have been only the aboveground portions of green vegetation. At other times of the year, their droppings may include nitrogen-fixing bacteria because of shifts in food habits. *Spermophilus parryi*, for instance, may eat mushrooms at certain times (Bee and Hall 1956) and thus may ingest nitrogen-fixing bacteria. *Cervus elaphus* eat hypogeous fungi part of the year (Trappe et al., unpublished data) and may ingest nitrogen-fixing bacteria. Other species, such as the plains pocket gopher (*Geomys bursarius*), feed on subterranean portions of plants and also ingest some soil while digging (Hamilton and Whitaker 1979); this behavior could also account for nitrogen-fixing bacteria in the feces.

Thus far, we have been able to identify only three of the isolated nitrogen-fixing bacteria: *Azospirillum* sp., *Clostridium butyricum*, and *C. beijerinckii*. *Azospirillum* sp. has been isolated from feces of the California red-backed vole and the northern flying squirrel (Li et al. 1986), and the creeping vole (*Microtus oregoni*) (Li and Maser, unpublished data). *Clostridium butyricum* has been isolated from feces of the deer mouse (Li et al. 1986), and *C. beijerinckii* from feces of the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*) (this study). These three species of nitrogen-fixing bacteria occur freely in the soil (Buchanan and Gibbons 1974, Hammann and Ottow 1976, Jones and Bangs 1985, Lakshmi et al. 1977). *Azospirillum* sp. can penetrate plant roots (Lakshmi et al. 1977, Patriquin and Döbereiner 1978), and *Azospirillum* sp. and *Clostridium* sp. have also been found associated with ectomycorrhizae of Douglas-fir (*Pseudotsuga menziesii*) (Li and Hung, Plant and Soil, in press).

Some species of yeast may increase nitrogen fixation in the presence of mycorrhizal fungi and thereby improve site productivity (Li et al. 1986, Maser et al. 1984). Yeast in the feces of mycophagous mammals may also be important because spore germination of some mycorrhizal-forming fungi is stimulated by extractives from other fungi, such as yeast (Fries 1966, 1982, Oort 1974).

Actinomycetes produce substances that are important in the formation of soil humus (Krassilnikov 1981), and humus, in turn, is important to the formation of mycorrhizae (Harvey et al. 1976, Kumuda et al. 1961, Maser et al. 1984). As stated by Linderman (1985), however, microbial interactions are complex, and actinomycetes are but a fraction of the complexity.

Mammals may play an important functional role in dispersing microorganisms vital to the ecosystem. Their potential importance is further suggested when these new data are coupled with the role of mammals in the dispersal of viable spores of mycorrhizal fungi, which are obligatory symbionts of most plants (Fogel and Trappe 1978, Kotter and Farentinos 1984, Maser et al. 1978, Rothwell and Holt 1978, Trappe and Maser 1977).

CONCLUSION

We reiterate that our survey was intended to ascertain the potential geographical scope of nitrogen-fixing bacteria (through acetylene reduction) in mammals. Our survey has some obvious deficiencies: for example, mammals were collected at different seasons and in different habitats, so standardizing was impossible. Isolating and identifying the nitrogen-fixing bacteria was extremely difficult; to our knowledge, no one has done this type of study before and laboratory techniques had to be modified (Li and Maser 1986). Finally, other microorganisms, such as yeasts and actinomycetes, are both poorly known and understood.

To study and understand the vast array of ecosystem processes require a carefully planned, interdisciplinary approach. As we learn more about mammal-habitat interactions, research must be aimed at the mammals as complex, functional links in the ecosystem. Understanding these dynamic linkages will help us to manage wisely both the mammals and their habitats to maintain or improve the health of the ecosystem.

ACKNOWLEDGMENTS

We thank G. E. Menkens, Jr. (Wyoming), R. L. Rausch (St. Lawrence Island, Alaska), J. O. Whitaker, Jr. (Indiana), P. D. Weigl (North Carolina–Tennessee border), and N. Wilson (Iowa), who sent us specimens; P. J. Bottomley (Department of Microbiology, Oregon State University, Corvallis), R. L. Rausch (Division of Animal Medicine, University of Washington, Seattle), R. F. Tarrant (Department of Forest Science, Oregon State University, Corvallis), and W. Thies (USDA Forest Service, Pacific Northwest Research Station), who critically reviewed the paper; and G. Bissell, who typed the various drafts.

This paper represents a partial contribution (No. 30) of the project entitled "The Fallen Tree—An Extension of the Live Tree." The project is cooperative among the U.S. Department of the Interior, Bureau of Land Management; U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station; Oregon State University, Department of Forest Science; U.S. Department of Agriculture, Agricultural Research Service; and Oregon Department of Fish and Wildlife.

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NOTES ON THE BIRDS OF COLD SPRING MOUNTAIN, NORTHWESTERN COLORADO

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ABSTRACT.—Observations are presented on 117 bird species seen in a 250-km^2 area of northwestern Colorado adjacent to Utah and Wyoming. Three previously unreported species and seven status changes are listed for the Rangely, Colorado, latilong block.

The bird life of northwestern Colorado and adjacent Utah and Wyoming is among the least known in the lower 48 states. Previous descriptions of this area resulted from short-term visits between the early 1900s and the mid-1960s (Cary 1909, Hendee 1929, Behle and Ghiselin 1958, Hayward 1967). The need for more ornithological fieldwork in this area became apparent with the advent of bird mapping schemes in Colorado and Utah based on latilong blocks (1 degree latitude and 1 degree longitude in size) (Chase et al. 1982, Walters and Sorensen 1983, respectively). These distribution plotting systems are valuable for providing an environmental data base for land-use planning and management, and, with some additional effort, for testing hypotheses about migration routes and distributions (see Bock 1984 for a similar example using 5-degree latilong blocks).

However, for latilong information to be useful, all blocks should have adequate and similar data bases. Unfortunately, these maps often show not the distribution of birds but the distribution of bird-watchers. For example, vesper sparrow (*Pooecetes gramineus*) and white-crowned sparrow (*Zonotrichia leucophrys*) were two of the most common breeding species on our study area (Table 1), yet they had not been recorded previously as breeding in the Rangely latilong block because of the paucity of bird-watchers. To supplement the inadequate ornithological records for northwestern Colorado and to increase the usefulness of the Colorado latilong data base, this report presents bird observations during a study of sage grouse (*Centrocercus urophasianus*) conducted in the northwestern corner of Colorado (northwest corner of the Rangely latilong block).

The sage grouse study was centered on Cold Spring Mountain approximately 1 km east of Utah, 7 km south of Wyoming, and immediately north of Browns Park National Wildlife Refuge, Moffat County, Colorado. Cold Spring Mountain (2,622 m) is part of the eastern extension of the Uinta Mountains, the largest east-west range in the Western Hemisphere. The topography of the study area varies from mountainous to rolling hills and mesas (1,820–2,909 m). Big sagebrush (*Artemisia tridentata*)–dominated rangeland and pinyon pine (*Pinus edulis*)–Utah juniper (*Juniperus osteosperma*) cover most of the study area. Quaking aspen (*Populus tremuloides*) woodland occurs on Cold Spring Mountain and in most canyons and mountainsides. Lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*) occur above 2,620 m on Middle Mountain (2,904 m) and Diamond Peak (2,909 m) near the Wyoming border. Snowfall at lower elevations occurs from November to April, whereas mountains in the study area often remain snow covered from late October to mid-May. This late snowmelt delays spring arrivals and nesting of many passerines on Cold Spring Mountain.

The annotated list (Table 1) is only of birds seen in the vicinity of Cold Spring Mountain, Diamond Peak, Middle Mountain, and Sugarloaf Flats; this is an area of approximately 250 km^2 covering the northwest corner of Colorado. The list of waterfowl and shorebirds is

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TABLE 1. List of bird species seen on Cold Spring Mountain and vicinity, northwestern Colorado.

Species	Status: Latilong study[1] (Changes, this study)	Abundance[2]	Dates seen[3]: Earliest	Dates seen[3]: Latest	Nesting dates[4]	Comments
Horned Grebe (*Podiceps auritus*)	M	U		10 Aug[5]		
Eared Grebe (*Podiceps nigricollis*)	B		20 May[5]			
Green-winged Teal (*Anas crecca*)	R	FC	30 Apr	6 Oct	Young:8 Jul	
Mallard (*Anas platrhynchos*)	R	C	31 May	10 Aug		
Northern Pintail (*Anas acuta*)	R	FC	30 Apr	10 Aug		
Blue-winged Teal (*Anas discors*)	B	FC	20 May	8 Jul	Young:8 Jul	
Northern Shoveler (*Anas clypeata*)	R	U	21 May	10 Aug		
American Wigeon (*Anas americana*)	R	FC	8 Jun	25 Aug	Young:8, 15 Jul	
Turkey Vulture (*Cathartes aura*)	B	FC	24 May	27 Sep		
Bald Eagle (*Haliaeetus leucocephalus*)	W	R	5 Apr	7 Nov		
Northern Harrier (*Circus cyaneus*)	R	FC	Seen every month			
Sharp-shinned Hawk (*Accipiter striatus*)	R	U		4, 26 Aug[5]		
Coopers Hawk (*Accipiter cooperii*)	B	U	30 Apr	13 Sep	Nest:30 Apr	
Northern Goshawk (*Accipiter gentilis*)	R(B)	U	30 Apr	19 Sep	Nest:30 Apr	
Swainson's Hawk (*Buteo swainsoni*)	B	FC	16 Aug	27 Sep		
Red-tailed Hawk (*Buteo jamaicensis*)	R	FC	5 Apr	19 Sep		
Ferruginous Hawk (*Buteo regalis*)	B	U	5, 6 Apr[5]			
Rough-legged Hawk (*Buteo lagopus*)	W	C	1 Nov	7 May		
Golden Eagle (*Aquila chrysaetos*)	R	FC	Seen every month		Nest:10 Apr	
American Kestrel (*Falco sparverius*)	R	FC	16 Apr	3 Oct		5 birds feeding on Mormon Crickets on 5 and 6 Aug
Merlin (*Falco columbarius*)	M		20 Aug[5]			
Prairie Falcon (*Falco mexicanus*)	B	FC	4 Apr	27 Jul		
Chukar (*Alectoris chukar*)	R	U	20,24 Jul; 8 Sep[5]			
Blue Grouse (*Dendragapus obscurus*)	R	FC	20 Apr	19 Sep	Young:19 Jul	
Sage Grouse	R	C	Seen every month		Nests:9(2 nests), 19, 20(2), 21, 31(2) May; second nests: 21, 31, May; 5, 17 June; young:many 3-week and older chicks after 12 Jul	
American Coot (*Fulica americana*)	B		30 May[5]			
Sandhill Crane (*Grus canadensis*)	M	R	4,5 Apr[5]			
Killdeer (*Charadrius vociferus*)	R	C	16 Apr	15 Aug	Many juvenile birds: 26–31 Jul	
American Avocet (*Recurvirostra americana*)	B		20 May[5]			
Greater Yellowlegs (*Tringa melanoleuca*)	M			23 Jul[5]		
Lesser Yellowlegs (*Tringa flavipes*)	M			4 Aug[5]		
Solitary Sandpiper (*Tringa solitaria*)	M			22 Jul[5]		
Spotted Sandpiper (*Actitis macularia*)	B	FC	31 May	17 Aug		
Western Sandpiper (*Calidris mauri*)	M	FC		13, 15 Aug[5]		
Long-billed Dowitcher (*Limnodromus scolopaceus*)	M	U		3 Aug[5]		
Common Snipe (*Gallinago gallinago*)	B	FC	26 Apr	23 Jul		
Wilson's Phalarope	b	FC	30 Apr	28 Jul		
Franklin's Gull (*Larus pipixcan*)	M		7 May[5]			
Mourning Dove (*Zenaida macroura*)	R	C	7 May	6 Oct		
Great Horned Owl (*Bubo virginianus*)	R	C	Seen or heard every month			
Northern Pygmy-Owl	(W)		Seen in Irish Canyon on 4 Feb 1984			
Long-eared Owl (*Asio otus*)	R	U	18 Jun	21 Sep		Hendee (1929) found a nest 28 May near the Little Snake River
Common Nighthawk (*Chordeiles minor*)	B	FC	31 May	25 Aug		
Common Poorwill	b(B, Hendee 1929)	FC	14 Jul	19 Sep		Most common second week in Aug; 20–40 birds/night
White-throated Swift	b	U	12 May	26 Sep		
Broad-tailed Hummingbird (*Selasphorus platycercus*)	B	C	3 Jun	26 Aug		
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	M	R	18 Apr	21 May		
Downy Woodpecker	b	FC	12 Apr	19 Sep		
Hairy Woodpecker (*Picoides villosus*)	M	FC	18 Jul	17 Aug		

Table 1 continued.

	Status		Dates seen[3]			
Species	Latilong study[1] (Changes, this study)	Abundance[2]	Earliest	Latest	Nesting dates[4]	Comments
Three-toed Woodpecker (*Picoides tridactylus*)	(n or b)		Seen on 24 July 1981 at Swede Spring on Cold Spring Mountain			
Northern Flicker (*Colaptes auratus*)	R	C	Seen every month			
Western Wood Pewee	b	FC	8 Jun	10 Aug		
Dusky Flycatcher (*Empidonax oberholseri*)	B	FC	7 Jun	18 Aug		
Gray Flycatcher (*Empidonax wrightii*)	B		3 Jun[5]			
Western Kingbird (*Tyrannus verticalis*)	b	R	8 May	15 Aug		
Horned Lark (*Eremophila alpestris*)	R	C	Seen every month		Nest: 5, 7 Jun	
Tree Swallow (*Tachycineta bicolor*)	B	C	11 Apr	5 Aug		
Violet-green Swallow (*Tachycineta thalassina*)	b(B)	C	21 May	3 Aug	Adult carrying fecal sac:23 Jun	
Barn Swallow (*Hirundo rustica*)	B	FC	15 Apr	5 Aug		
Steller's Jay (*Cyanocitta stelleri*)	R	FC	19 Jul, 13 Sep[5]			
Scrub Jay (*Aphelocoma coerulescens*)	R	FC	Seen every month			
Pinyon Jay (*Gymnorhinus cyanocephalus*)	R	C	Seen every month			More than 50 birds feeding on Mormon Crickets 5 Aug
Clark's Nutcracker (*Nucifraga columbiana*)	R	C	Seen every month			Ten birds feeding on Mormon Crickets 5 Aug
Black-billed Magpie (*Pica pica*)	R	C	Seen every month			More than 100 birds feeding on Mormon Crickets 5 and 17 Aug
American Crow (*Corvus brachyrhynchos*)	R	FC	Seen every month			
Common Raven (*Corvus corax*)	R	FC	Seen every month			
Black-capped Chickadee	W(N)	FC	20 Feb, 14 Apr, 3 May, 15, 17 Aug; 19 Sep[5]			
Mountain Chickadee (*Parus gambeli*)	R	FC	Seen every month			
Plain Titmouse (*Parus inornatus*)	B	FC	3, 4, 8 May[5]			
Bushtit	b		5 May[5]			
Red-breasted Nuthatch (*Sitta canadensis*)	R	U	29 Jun	26 Aug		
White-breasted Nuthatch (*Sitta carolinensis*)	R		21 May[5]			
Rock Wren (*Salpinctes obsoletus*)	B	U	Seen every month			
House Wren (*Troglodytes aedon*)	B	C	4 May	24 Aug	Fledglings:27 Jun	
Ruby-crowned Kinglet (*Regulus calendula*)	M	U	17, 21 May[5]			
Blue-gray Gnatcatcher (*Polioptila caerulea*)	B		15 Jun[5]			
Mountain Bluebird (*Sialia currucoides*)	B	FC	17 Mar	3 Oct		
Townsend's Solitaire (*Myadestes townsendi*)	M	FC	4 May	3 Oct		
American Robin (*Turdus migratorius*)	R	FC	Seen every month at lower elevations		2 nests with 4 eggs:5 Jun	
Northern Mockingbird (*Mimus polyglottos*)	b	UC	6 Jun	3 Oct		
Sage Thrasher (*Oreoscoptes montanus*)	B	FC	6 Apr	25 Aug		
Water Pipit (*Anthus spinoletta*)	(b or M)		3 Oct 1981[5]			4 birds near Arthur's Reservoir
Bohemian Waxwing (*Bombycilla garrulus*)	W		3 Nov[5]			
Northern Shrike (*Lanius excubitor*)	W	U	1, 7 Nov[5]			
Loggerhead Shrike (*Lanius ludovicianus*)	B	U	31 May, 4 Jun[5]			
European Starling (*Sturnus vulgaris*)	R	C	Seen every month			
Warbling Vireo (*Vireo gilvus*)	b(B)	FC	31 May	19 Sep	2 nests:19 Jun	
Yellow Warbler (*Dendroica petechia*)	B	FC	15 Jun	17 Aug		
Yellow-rumped Warbler (*Dendroica coronata*)	B	U	21 May	17 Aug	Adult feeding young: 14 Jul	
Black-throated Gray Warbler (*Dendroica nigrescens*)	B	U	17, 21 May[5]			
MacGillivray's Warbler (*Oporornis tolmiei*)	B	FC	9 Jun	19 Sep		
Common Yellowthroat (*Geothlypis trichas*)	B		15 Jun[5]			
Wilson's Warbler (*Wilsonia pusilla*)	B	FC	17, 18, 25 Aug			
Western Tanager	b	FC	10 Aug[5]			
Black-headed Grosbeak (*Pheucticus melanocephalus*)	B	FC	1 Jun	17 Aug	Female with food: 27 Jul	

Table 1 continued.

	Status		Dates seen[3]			
Species	Latilong study[1] (Changes, this study)	Abundance[2]	Earliest	Latest	Nesting dates[4]	Comments
Lazuli Bunting (*Passerina amoena*)	b		11 Aug[5]			
Green-tailed Towhee (*Pipilo chlorurus*)	B	FC	4 May	13 Sep	Nest with 4 eggs: 5 Jun; young:20 Jun	
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	B	U	1 May	7 Jun		
American Tree Sparrow (*Spizella arborea*)	W	FC	3 Nov	4 Apr		
Chipping Sparrow (*Spizella passerina*)	B	FC	16 Jun	25 Aug		
Brewer's Sparrow (*Spizella breweri*)	B	C	31 May	19 Sep	Nest:8, 21 Jun; young:23 Jun, 24 Jul	One of the most common breeding species
Vesper Sparrow	b(B)	C	25 Apr	26 Sep	Eggs:21 Jun; fledglings:27 Jun, 23–31 Jul	One of the most common breeding species
Lark Sparrow (*Chondestes grammacus*)	B	FC	8 May	4 Jun		
Sage Sparrow (*Amphispiza belli*)	B	R	3, 6, 30 Apr[5]			
Savannah Sparrow (*Passerculus sandwichensis*)	b		17 Aug[5]			
White-throated Sparrow (*Zonotrichia albicollis*)	M		31 May[5]			
White-crowned Sparrow	M(B)	C	10 May	26 Aug	Nests:1 Jun eggs:1,5 Jun young:15 Aug	Very common breeding species
Dark-eyed Junco (*Junco hyemalis*)	R	FC	Seen every month		Nest:16 Jun young:28 Jun	
Red-winged Blackbird (*Agelaius phoeniceus*)	R	C	20 Apr	19 Sep		
Western Meadowlark (*Sturnella neglecta*)	R	FC	13 Apr	3 Oct		
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	B	FC	2 May	19 Jul		
Brewer's Blackbird (*Euphagus cyanocephalus*)	B	FC	1 May	19 Sep	Nest:19 Jun	More than 100 birds feeding on Mormon Crickets on 6, 18 Aug
Brown-headed Cowbird (*Molothrus ater*)	B	FC	2 May	4 Sep		
Rosy Finch (*Leucosticte arctoa*)	W	U	1 Nov	12 Apr		
Cassin's Finch (*Carpodacus cassinii*)	R	FC	16, 18 May[5]			
Red Crossbill (*Loxia curvirostra*)	b		31 May[5]			
Pine Siskin (*Carduelis pinus*)	W	FC	1 Nov	30 Apr		
American Goldfinch (*Carduelis tristis*)	B		30 May[5]			

[1] Status given in Chase et al. (1982). R = Resident year-round (breeds); N = Nonbreeder present year-round, or a year-round resident whose breeding has not been documented; B = Breeding (documented); b = Likely breeder; W = Winter visitor; M = Migrant; blanks indicate no record.

[2] Abundance categories: C = Common; FC = Fairly common; U = Uncommon; R = Rare; Irr = Irregular. Abundance was estimated in this study, and categories are from Chase et al. (1982). A blank indicate too few data to evaluate.

[3] Dates observed represent our records and may not be indicative of actual arrival/departure dates for migrants and summer residents in the entire region.

[4] Nesting dates are presented only where information is known.

[5] Only date(s) seen.

relatively short because most of these species stop at better habitat in Browns Park; Cold Spring Mountain is mostly xeric, with the exception of six small reservoirs. A notable aspect of the species list is that the breeding status of several relatively common species remains to be documented. Future field workers in this area should attempt to document breeding for Wilson's phalarope (*Phalaropus tricolor*), northern pygmy owl (*Glaucidium gnoma*), common poorwill (*Phalaenoptilus nuttallii*), white-throated swift (*Aeronautes saxatalis*), downy woodpecker (*Picoides pubescens*), western wood pewee (*Contopus sordidulus*), western kingbird (*Tyrannus verticalis*), black-capped chickadee (*Parus atricapillus*), bushtit (*Psaltriparus minimus*), and western tanager (*Piranga ludoviciana*), among others. The northern pygmy owl, three-toed woodpecker, and water pipit were recorded for the first time from this area.

ACKNOWLEDGMENTS

Financial support for this project was provided by the Colorado Division of Wildlife through Federal Aid to Wildlife Restoration Project W-37-R and the Rob and Bessie Welder Wildlife Foundation, Sinton, Texas.

The support of these agencies and organizations is gratefully acknowledged. A draft of the manuscript was reviewed by C. M. Haynes and W. D. Snyder. C. E. Braun kindly reviewed drafts of the manuscripts and provided access to his field notes. J. W. Hupp, T. E. Olsen, and D. Ward also provided records of their observations. This is Welder Wildlife Foundation publication number 303.

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LIFE STRATEGIES IN THE EVOLUTION OF THE COLORADO SQUAWFISH (*PTYCHOCHEILUS LUCIUS*)

Harold M. Tyus[1]

Abstract.—The Colorado squawfish, a large predaceous cyprinid, is a generalist species adapted to the large seasonal water fluctuations, low food base, and changing riverine subsystems of the Colorado River. Extant at least as early as the Miocene epoch, *Ptychocheilus* has survived by incorporating life strategies to deal with changing climates varying from arid to pluvial. Migration and long-term movement patterns appear to have evolved as tactics to perpetuate a grand reproductive strategy for exploiting the changing habitats and general environmental conditions of the late Cenozoic era. Accordingly, high mobility of a large fish would aid in selection of optimum spawning, nursery, and adult habitats in the dynamic lacustrine/riverine system that existed at that time. A spatial separation of life stages thus produced would aid in the reduction of intraspecific competition. Large size, long life, and late spawning of *Ptychocheilus* indicate that mortality of young must be disproportionately high compared to that of the adult form. Growth to a large size should reduce predation by other fishes and, once attained, would facilitate long distance movement for reproduction, feeding, and other purposes. Such a strategy, formerly highly adaptive, may now be implicated in the decline of this species in controlled riverine systems.

The genus *Ptychocheilus* includes the largest cyprinids in North America. Represented by four species today, the largest of these, the Colorado squawfish (*Ptychocheilus lucius* Girard) formerly grew to a size of about 1.8 m and 45 kg (Miller 1961). Endemic to the Colorado River Basin, this fish, once distributed throughout the basin, has declined since the 1930s and is today restricted to the upper Colorado River Basin, where it is classified as endangered by the U.S. Fish and Wildlife Service (1973, 1974). The loss of the Colorado squawfish from parts of the Colorado River is apparently related to major water developments that have ostensibly reduced *P. lucius* to about 25% of its former range (Tyus 1984). Although many workers have postulated man-induced changes in riverine conditions as primary factors in the reduction of the range and abundance of this species (Miller 1961, Holden and Wick 1982, Ono et al. 1983), a lack of basic knowledge about its life history, especially in locations where the fish has been lost (Minckley, 1973), has made these implications impossible to prove. Recent research in the Green River Basin (Fig. 1) by the U.S. Fish and Wildlife Service (Tyus and McAda 1984) resulted in the first discovery of a spawning grounds of this species in 1981 and identified migrations and movements as important factors in the reproductive strategy of this species. These findings have been substantiated by the work of Haynes et al. (1984), Wick et al. (1983), Tyus (1985), and others.

With the present knowledge of the life history requirements of *P. lucius*, it is now possible to relate its apparent life strategies with its evolution and adaptations to conditions in the Colorado River Basin. In so doing I have drawn heavily from the works of G. R. Smith (1981) and M. L. Smith (1981), who presented the background on late Cenozoic climates and adaptations of the southwestern fish fauna, particularly *P. lucius*, upon which this work is based.

Climate and Adaptation of *Ptychocheilus*

The cyprinid fishes apparently arrived in the New World from Asia in the Miocene epoch, and fossil *Ptychocheilus* species similar to modern *Ptychocheilus lucius* have been reported from the middle Pliocene in the Colorado River system of northern Arizona (Miller 1961). *Ptychocheilus* had widespread distribution in the Pliocene, as evidenced by fossils in Lake Idaho (Smith 1975), the Great Basin (G. Smith 1981), and Arizona (Miller 1961). Furthermore, the similarity between the Pliocene fossils and modern forms suggests that the adaptation to swift water habitat had

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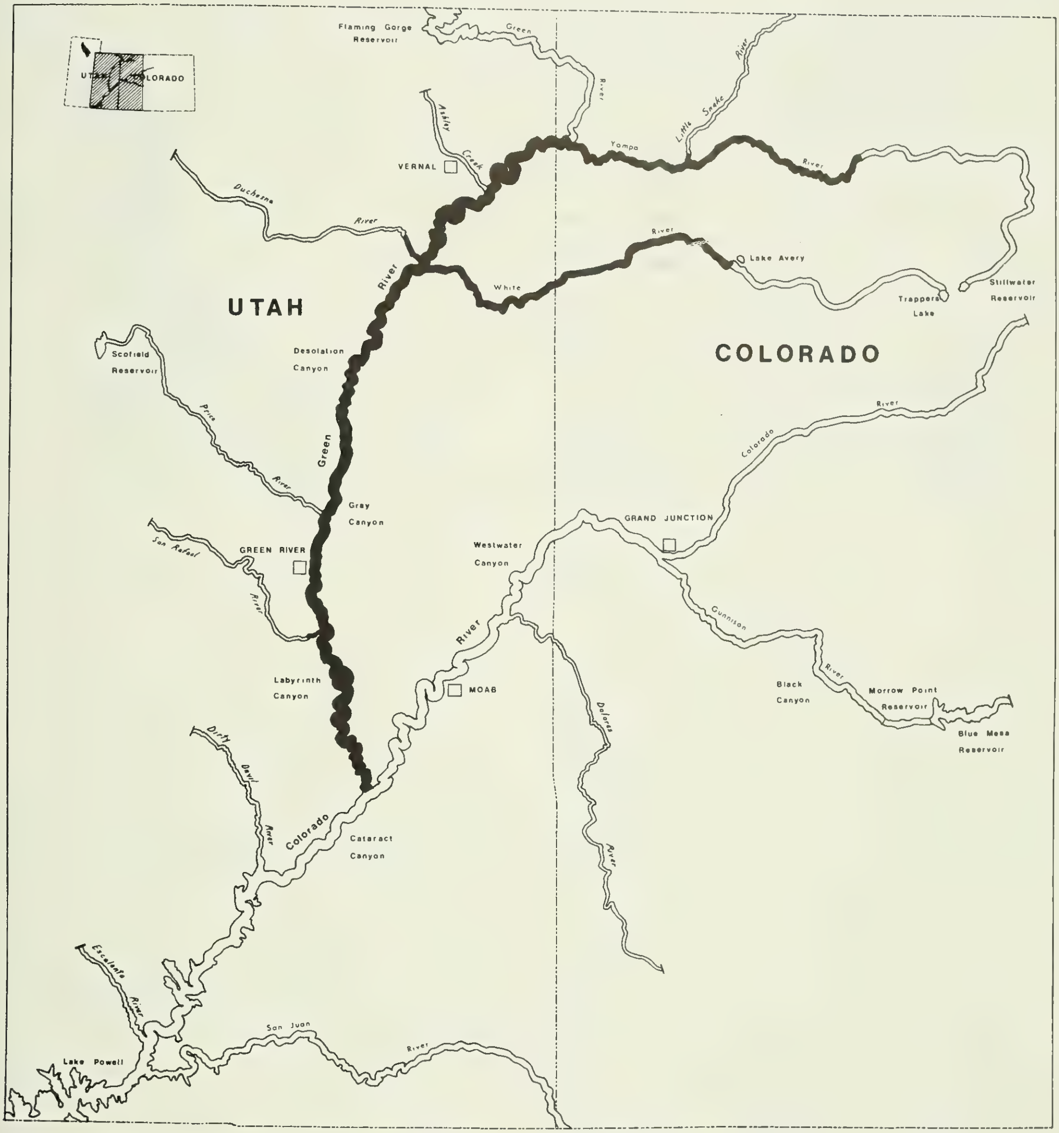
Flaming Gorge Reservoir
Green River
UTAH
COLORADO
Ashley Creek
VERNAL
Yampa River
Little Snake River
Duchesne River
White River
Lake Avery
Trappers Lake
Stillwater Reservoir
UTAH
COLORADO
Desolation Canyon
Scofield Reservoir
Price River
Green River
Gray Canyon
GREEN RIVER
San Rafael River
Colorado River
GRAND JUNCTION
Westwater Canyon
Gunnison River
Black Canyon
Morrow Point Reservoir
Blue Mesa Reservoir
River
MOAB
Labyrinth Canyon
Dolores River
Dirty Devil River
Colorado
Cataract Canyon
Escalante River
San Juan River
Lake Powell

Fig. 1. Upper Colorado River Basin and Green River study area (shaded).

occurred in *Ptychocheilus* by the mid-Pliocene (Miller 1961). Nonetheless, the largest *Ptychocheilus* reported in the fossil record lived in Pliocene Lake Idahò (Smith 1975), indicating that *Ptychocheilus* successfully utilized both riverine and lacustrine systems.

The Southwestern United States is more arid today than in the Late Cenozoic, and this increasing aridity no doubt resulted in the loss or reduction of lacustrine habitats and the extinction of lake dwelling salmonids and centrarchids from the Colorado River system. This change was progressive from the Pliocene, when a system of lakes covered the lower and upper Colorado River Basins, and persisted during pluvial periods until the Pleistocene. During this epoch the life history of fishes was remarkably impacted by such long pluvial periods interrupted by short periods of desert conditions (G. Smith 1981).

An evaluation of the fish fauna of the Colorado River in recent times (before introductions by man) might lead one to conclude that the isolated drainages and depauperate faunas of today reflect Cenozoic conditions. They do not. Instead, the fossil record shows that the large regional desert environs of the Southwest are "geologically new" (M. Smith 1981) and not typical in the development of life history attributes of the fish fauna. This has led M. Smith (1981) to propose that the ecological history of the fishes suggests they should be considered generalists, not specialist species. In this case *Ptychocheilus* would have developed the capability to utilize both riverine and lacustrine habitat depending upon the climatic conditions prevailing.

During the late Cenozoic, estuarine conditions in the lower basin and widespread lacustrine habitat during pluvial periods would provide eutrophic conditions that could be exploited by a top carnivore like *Ptychocheilus*. These same areas, however, might not have provided the best spawning and nursery conditions because of adverse environmental (e.g., oxygen, substrate) and biological (e.g., predation) factors. If *Ptychocheilus* could move between preferred spawning and feeding areas, it might have the best of both. G. Smith (1981) proposed that migration would be a major adaptation to dry seasons for intermountain desert fishes like *Ptychocheilus*, and that emigration of young fish to unoccupied areas might be selected for in genotypes. If movement and/or migration is highly adaptive, this behavior would have evolved with modern *Ptychocheilus*.

Another consideration in the evolution of *Ptychocheilus* is large adult size. The popular notion of a richer food supply in the recent past is interesting, but is probably not the factor driving the adaptation to large body size. In the intermountain desert G. Smith (1981) noted the tendency for large habitats to produce large fishes, and, in view of the low food ration available, suggested that life history adaptations to the growing season and differential mortality are primary determinants. Species experiencing low adult mortality that grow larger and live longer could be expected to produce a large number of offspring in the desirable wet years and outcompete those species that sacrifice size and longevity for early reproduction. Since *Ptychocheilus* and various salmonids are the only large native predators throughout most of the Colorado River, survival to a moderate size would insure low adult mortality. Thus, modern *Ptychocheilus* should display rapid growth and delayed reproduction to favor a large adult size if these attributes have selective advantage.

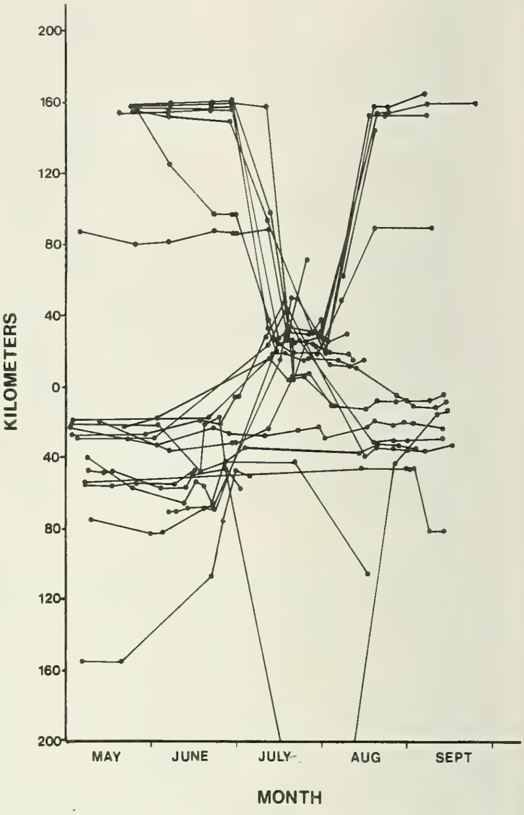

Fig. 2. Movement of radiotelemetered Colorado squawfish, Yampa and Green rivers, 1983 and 1984 (after Archer et al. 1985). Mouth of Yampa River = 0 km.

STRATEGIES OF *PTYCHOCHEILUS LUCIUS*

As stated previously, modern *Ptychocheilus* exists today in conditions different from those in which it evolved. An examination of the known life history attributes of *P. lucius* contrasted with the conditions and potential adaptations to late Cenozoic conditions may reveal life strategies in its evolution that would aid in its survival and potential recovery.

Migration, Movement, and Habitat Selection

As predicted by G. Smith (1981), *P. lucius* makes extensive use of migration in its life

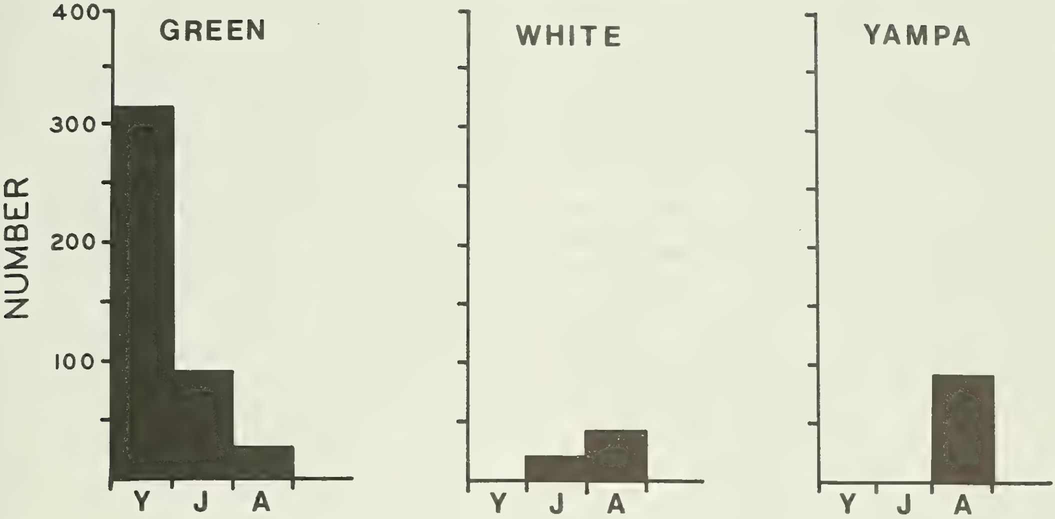

Fig. 3. Catch of Colorado squawfish from the Green, White, and Yampa rivers (Tyus et al. 1982, Miller et al., *White River*, 1982; *Yampa River*, 1982. Y=young of year, J=juveniles, A=adult.

strategy, and adults have been documented as homing to desirable spawning sites (Tyus 1985). Figure 2 illustrates the spectacular spawning migrations to the Yampa River spawning site in 1983 and 1984. Migrations of young are not so easily documented, but downstream transport of larvae have been noted by Haynes et al. (1984) and Tyus and McAda (1984). A net long-term movement of juveniles must occur to populate adult areas upstream, probably in the late young-adult stage, is indicated by collection data (Tyus et al. 1982). Figure 3 illustrates that, in the mainstem Green River, young *P. lucius* are relatively abundant and juveniles common; however, in the major tributaries (White and Yampa rivers) where adults predominate, juveniles are rare and young absent during most of the year.

Habitat selection appears to be the driving force for migration. Hence, adults move up to 200 km to spawn in white-water canyons. After hatching, young larvae can drift downstream and occupy warm shallow habitats where rapid growth is possible. These movements also aid in reducing intraspecific predation since the adults and young tend to concentrate in different river sections. Recent studies (Archer et al. 1985) also show that during flood periods adult *P. lucius* move out of the river banks and occupy flooded bottoms, where they presumably feed on terrestrial wildlife such as small mammals (Beckman 1952).

Potamodromous migrations of cyprinid fishes are not well documented for North American forms, at least not for migrations of 100 km or more. Such migrations are not uncommon in flood plain rivers in other parts of the world (Welcomme 1979). *Ptychocheilus lucius* appears to take advantage of river transport at the end of the flood period for the dispersal of young from the spawning grounds downstream into productive nursery habitat (Tyus and McAda 1984). This behavior resembles some South American freshwater species in this regard, and it has been noted that in Africa potamodromy may protect the young from predation and secure dispersal over the river basin (Welcomme 1979).

Reproductive Adaptations

The spawning of *P. lucius* occurs in middle to late summer under a decreasing flow regimen. This is unusual among most stream fishes, which spawn in the spring and early summer with rising water levels. As with other potamodromous riverine species, timing of reproduction is very important, and studies of spawning *P. lucius* (Archer et al. 1984) indicate the fish apparently times its spawning to coincide with the descending limb of the hydrograph, a time when downstream transport of young would distribute them into the shallow nursery habitat that forms during this period in the Green River. Such a temporal adaptation fits in well with the life strategy of *P. lucius*, for the length of exposure of *P. lucius* young to predators is reduced. This reduced time for the young to feed is balanced by delivering them into ideal conditions for growth.

This species selects highly oxygenated white-water rapids and riffles for spawning sites that may be 100 km or more from their preferred adult habitat at that time (Archer and Tyus 1984). Although the mechanism by which these fish congregate in spawning areas is unknown, a homing response (Tyus 1985) could result in sufficient breeding adults returning to a small area to insure good genetic recombination and, therefore, maintain a high degree of genetic diversity in the population.

Natural Adaptations and Controlled Systems

Ptychocheilus lucius evolved as a species adapted to conditions existing at the close of the Cenozoic era. These same adaptations enabled it to compete and survive in the isolated and depauparate Colorado River Basin in the Holocene until the coming of man. Although cause-effect relationships between water development and the decline of the Colorado squawfish have not been proven de facto, it is generally agreed that such development negatively affects the fish (Ono et al. 1983). The life strategies developed from comparing life history attributes of *P. lucius* with late Cenozoic climatic, geologic, and fossil records suggest that evolving life strategies that adapted *P. lucius* to the natural system would ill befit the fish to a controlled system.

Paramount in the life strategy of *P. lucius* is the need for unimpeded movement within the riverine system, and blockage of major stream sections where *P. lucius* occurs has resulted in the extirpation of the fish from these areas (Tyus 1984). In addition, the downstream transport of larva and establishment of shallow euphemeral embayments for nursery areas are needed, and a proper discharge regime must be maintained for spawning and rearing of young.

Life strategies proposed herein for *P. lucius* need refinement and further substantiation. Only by understanding these strategies, however, can we place its evolution in proper context and provide for its future.

ACKNOWLEDGMENTS

The research upon which concepts in this paper are developed was supported, in part, by the Fish and Wildlife Service, Bureau of Reclamation, National Park Service, Bureau of Land Management and the States of Colorado and Utah. Principal field personnel included C. W. McAda, B. D. Burdick, K. C. Harper, R. M. McNatt, J. J. Krakker, Jr., W. B. Harned, E. J. Wick, and D. L. Skates. Administrative direction was furnished by W. H. Miller and D. L. Archer. My thanks are given to W. R. Hansen and R. L. Jones, who provided suggestions for the manuscript.

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PARASITES OF THE WOUNDFIN MINNOW, *PLAGOPTERUS ARGENTISSIMUS*, AND OTHER ENDEMIC FISHES FROM THE VIRGIN RIVER, UTAH

Richard A. Heckmann[1], James E. Deacon[2], and Paul D. Greger[2]

ABSTRACT.—Two hundred woundfin minnows, *Plagopterus argentissimus*, from four sites along the Virgin River, Utah, were examined on two dates during summer 1985. The foreguts of 211 woundfin and variable numbers of other fishes from the Virgin River near Beaver Dam Wash, Arizona, and Mesquite, Nevada, were examined for cestodes on four dates throughout 1979. Seven parasites were found in *P. argentissimus: Posthodiplostomum minimum* (metacercariae), *Diplostomum spathaceum* (metacercariae), *Bothriocephalus acheilognathi, Gyrodactylus* sp., *Lernaea cyprinacea, Trichodina* sp., and *Ichthyophythirius multifiliis.* Fungal infections were noted on two fish during the study. Seventeen Virgin River roundtail chub, *Gila robusta seminuda*, were examined from two of the four sites in 1985 and 64 specimens from Beaver Dam Wash were examined in 1979. *Gila robusta seminuda* was infected with *Posthodiplostomum minimum* (metacercariae) and *Bothriocephalus acheilognathi*, the Asian fish tapeworm. This cestode probably gained entrance into the ichthyofauna of the Virgin River from red shiners, *Notropis lutrensis*, and has the potential of being very detrimental to the endemic and endangered fishes of the Virgin River. Parasite loads were correlated with water quality and habitat disturbance, with highest number and frequency occurring in "disturbed" sites. Low river flows and increased total dissolved solids appear to be associated with a higher parasite frequency and mean number in fishes of the Virgin River. These data represent the first known published records for parasites of the woundfin minnow and Virgin River roundtail chub.

There is a paucity of information on the parasitofauna of the woundfin minnow, *Plagopterus argentissimus,* and other species of fish from the Virgin River, Utah-Arizona-Nevada. Many of the fishes in the Virgin River are endemic and have been listed as endangered species, the woundfin included. Hoffman (1967) lists no parasites for the woundfin. Other common fishes in the Virgin River drainage include the Virgin roundtail chub, *Gila robusta seminuda;* speckled dace, *Rhinichthys osculus;* Virgin spinedace, *Lepidomeda mollispinis;* desert sucker, *Catostomus clarki;* flannelmouth sucker, *Catostomus latipinnis;* and the introduced red shiner, *Notropis lutrensis*. Parasites of these later species are also poorly known (Hoffman 1967). Parasites can have adverse effects on fish populations. Changes in incidence, intensity, or parasite species infecting or infesting a host can provide important clues to the health and status of fish host populations. To understand management options, it is essential to also know the life cycle of the parasite and its effects at various levels of infection. For example, parasitism can be responsible for reduced growth rates, reduced egg production, poor swimming performance, aberrant behavior, etc. (David 1947, Dogiel 1958, Hoffman 1967).

The primary objectives of this study were as follows:

1. Identify the species of parasites inhabiting the woundfin minnow at selected sites in the Virgin River in Utah.
2. Determine the frequency of occurrence, abundance, and temporal variation of parasites for *P. argentissimus* in the summer during the normal period of low flow.
3. Determine the relationship between parasitism and the immediate habitat of the host.
4. Determine the pathogenicity of the parasite to the host.

In a previous study conducted during 1979 (Greger 1983), woundfin minnows examined during February and June near Beaver Dam Wash, Arizona, were not parasitized by cestodes. Cestodes were present, however, in the foreguts of *P. argentissimus* and increased in both number and frequency from September to December. Frequency of infection of woundfin with cestodes was much less near Beaver Dam Wash, Arizona, than was true further downstream in Nevada. This suggested that woundfin may be more vulnerable to parasitism in an agriculturally disturbed habitat than in a more natural environment. Because the Virgin River near St. George,

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Utah, exhibits similar agricultural disturbances, our hypothesis was that the parasite load in the fish population near St. George would be higher than in the less disturbed sections of Virgin River in Utah.

The life cycles of cestodes and other parasites of fishes from the Virgin River have not been determined in detail. In general, fishes can be both definitive and intermediate hosts for cestodes. Reproductively mature adult cestodes present in fish will release eggs from gravid proglottids while in the intestine of the host. The eggs passs through the host's anus and may settle in the stream sediments. For many cestodes, increasing temperature causes the operculate eggs to hatch, releasing a ciliated coracidium (motile oncosphere). Cyclopoid copepods (first intermediate host) ingest these larvae and become infected. The oncosphere sheds its ciliated coat in the gut of the copepod and burrows through the intestinal wall to the hemocoel, where it develops into a procercoid larvae (Cheng 1973). This mesacestode-type larva cannot become infective to a definitive host for about two to three weeks, until cercomer formation (Cheng 1973). If a fish ingests an infected copepod, the adult cestode may commence development in the intestine of the host. Although larval (pleroceroid) development in a second intermediate host (such as a smaller fish) is possible, it is unlikely to occur in the Virgin River ichthyofauna, since no primarily piscivorous fishes are present. It seems more probable that development of the adult cestode in Virgin River fishes occurs following ingestion of an infected copepod. Direct development of the adult pseudophyllidean cestode *Eubothrium salvelini* following ingestion of infected *Cyclops* sp. by Sockeye salmon, *Oncorhynchus nerka*, has been reported by Smith (1973) from a lake in British Columbia.

The effects of adult cestodes upon fish hosts have not been studied in detail. Rees (1967), after an extensive review of the literature, reached no definitie conclusions regarding the lethal effects of adult cestodes. Other investigators have suggested that adverse effects are considerable. Smith (1973) reported that noninfected salmon smolts grew 5%–7% longer and 17%–24% heavier than infected smolts. Field observations and swimming performance tests suggested cases of reduced swimming abilities and earlier fatigue in salmon and trout infected with helminths (Smith and Margolis 1970, Heckman 1983). These data also demonstrate some nutritional or growth impairments for infected fish. Other researchers (Wardle 1933, Dogiel 1958, Dombroski 1955) have reported that adult pseudophyllidean cestodes can affect host nutrition and survival. Severe occlusion (impaction) of the gut has been reported for infected salmon (Dogiel 1964) and appeared to affect the nutritional status in severe cases. Impaction by parasites would also affect reproductive potential. Williams and Halvorsen (1971) negated the belief that contents of the fish host intestine represent an unlimited source of food for cestodes. Impaction and reduced growth and vigor would also reduce reproductive potential.

Other indirect effects of cestode adults on their hosts have been demonstrated in the laboratory. Boyce and Clarke (1983) determined that Sockeye salmon yearlings infected with tapeworms had a reduced ability to adapt to seawater as evidenced by increased mortality and elevated plasma sodium levels. Boyce and Behrens-Yamada (1977) also reported Sockeye salmon juveniles infected with the same cestode, *Eubothrium salvelini*, to be more sensitive to zinc toxicity. These effects could make the infected fish less vigorous and more susceptible to predation during its seaward migration.

The Asian fish tapeworm, *Bothriocephalus acheilognathi*, introduced into this country by imports of grass carp, has been described as a dangerous parasite in Europe (Bauer et al. 1981). This cestode has apparently become established in the ichthyofauna of southern Utah.

The most common fish parasite found in this survey was the metacercarial state of the digenetic trematode, *Posthodiplostomum minimum*. "Black spot," for example, is caused by metacercarie found in melanin-pigmented cysts in the skin. This larval stage of flukes may be found in all tissues of fish (Spall and Summerfelt 1969b).

MATERIALS AND METHODS

The 1979 collections were made in February, June, September, and December near Beaver Dan Wash, Arizona, and Mesquite, Nevada (Fig. 1). At each location, the foregut

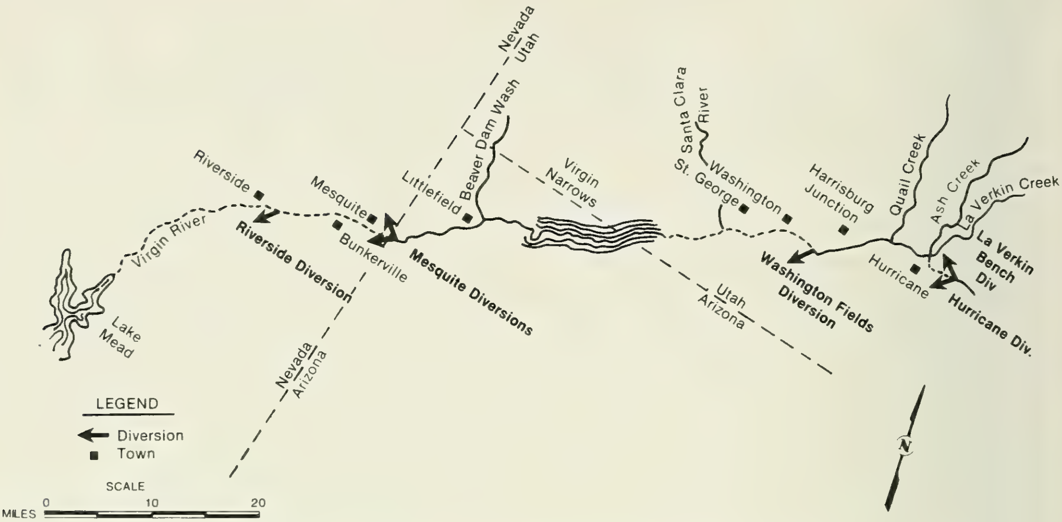
Nevada
Utah
Beaver Dam Wash
Virgin Narrows
Santa Clara River
St. George
Washington
Harrisburg Junction
Quail Creek
Ash Creek
La Verkin Creek
La Verkin Bench Div
Hurricane
Hurricane Div.
Washington Fields Diversion
Utah
Arizona
Littlefield
Mesquite
Bunkerville
Mesquite Diversions
Riverside
Riverside Diversion
Virgin River
Lake Mead
Nevada
Arizona
LEGEND
Diversion
Town
SCALE
MILES
0
10
20
N

Fig. 1. Fish sampling sites along the Virgin River, Utah, Nevada, Arizona, for this study.

TABLE 1. Rating scale to indicate approximate density of the metacercarial infection in Virgin River fishes.

Assigned scale number	Average number of metacercariae per microscopic field at 20X
0	None
1	1–9
2	10–19
3	20–29
4	30–39
5	40–TNTC

of 22–34 woundfin and variable numbers of other species was examined. Because the 1979 study was conducted as a part of a study of food habits (Greger 1983), we looked only for cestodes in the foregut.

The 1985 collections were taken from the Virgin River on 27 and 28 July and 23, 24, 25, and 31 August 1985. Collections were made about 1/4 mile downstream from the inflow of the Santa Clara River, at Twin Bridges, about two miles below Berry Springs, and at Hurricane Bridge in Utah, and downstream in Nevada near Mesquite (Fig. 1). At each location 23–25 *P. argentissimus* and variable numbers of other fish species were examined. At Mesquite we examined 88 red shiners.

In 1985 external examination for parasitism was made immediately following death of the fish. Scrapings of mucus and epithelial cells were taken from the gill surface, the base of the fins, and the lateral surface of the body. Scrapings were mixed in physiological saline and examined at 100X and 430X. Blood samples were obtained from peripheral circulation on microscope slides, air dried, and later stained (Giemsa-Wright combination) prior to examination at 430X and 1000X. Each blood slide was examined for a minimum of 10 minutes.

The abdominal cavity was opened ventrally and internal organs were examined. Each organ was removed and placed in a saline solution prior to examination with a dissecting microscope. Eye tissues, including the lens, were also examined.

Cestodes were excised from the intestinal tract, enumerated and fixed in AFA. Some individual worms were prepared for examination by scanning electron microscopy by fixation in 3% gluteraldehyde with an acrolein buffer.

Viscera and gills from two woundfin from each of the four sampling locations were fixed in buffered 10% formalin and prepared for tissue evaluation at the Brigham Young University laboratory. These samples were processed by standard methods, stained, and examined closely to evaluate parasite pathology. Two stains, trichrome, and hematoxylin and eosin were used for the tissue sections.

During the first day of study it was noted that many fish were heavily parasitized by metacercariae of the trematode, *Postho-*

TABLE 2. Summary of parasite data from woundfin captured at each of four locations 27–28 July (N = 25) and 23–25 August (N = 23). August data are in parentheses.

Sample location	Average total length		*Posthodiplostomum* Percent		*Posthodiplostomum* Average scale number		Number with other disease problems	
Twin Bridges	76.4	(75.7)	100	(96)	5.0	(4.0)	3/25[a]	(5/23[c])
Santa Clara inflow	69.0	(69.8)	100	(100)	3.6	(2.7)	1/25[b]	(5/23[d])
Hurricane Bridge	74.1	(80.8)	44	(57)	1.0	(1.0)	0	(0)
Berry Springs	70.7	(64.9)	8	(22)	<1.0	(<1.0)	0	(1/23[e])

[a] 3/25 Eye fluke (metacercariae), *Diplostomum spathaceum*, fungal growth, dorsal fin.

[b] 1/25 Fungal growth, dorsal fin, skin erosion and fungal growth, pectoral fin; *Gyrodactylus*, gills.

[c] 5/23 Eye fluke (metacercariae), *Diplostomum spathaceum*, Roundworm, intestine, 3 fish. *Trichodina*, ciliated protozoan (gills), Anchor worm, *Laernea*, 2 fish.

[d] 5/23 Eye fluke (metacercariae), *D. spathaceum*, Anchor worm, *Laernea*, 3 fish. *Trichodina*, ciliated protozoan (gills), 2 fish.

[e] 1/23 *Trichodina*, ciliated protozoan (gills).

diplostomum minimum. A rating scale was developed to represent different densities of infection (Table 1).

RESULTS

Results of the parasitological examination are presented in Tables 2 to 6. These data show that the "disturbed" segments of the river (Mesquite, Twin Bridges, and Santa Clara inflow) carried a heavier parasite load than in undisturbed segments (Beaver Dam Wash, Hurricane Bridge, and Berry Springs) (Deacon and Hardy 1984). There is further indication that the trematode parasite, *Posthodiplostomum minimum*, in woundfin minnows in the "undisturbed" segment of the Virgin River in Utah may have increased slightly from July to August 1985 (Table 2). Whereas the trematode, *Posthodiplostomum minimum*, was clearly the major parasite infecting woundfin, other parasites were detected on some individuals (Table 2).

A limited number of other fish were also examined for parasites (Tables 3 to 6). Of greatest concern was the presence of the Asian tapeworm, *Bothriocephalus acheilognathi*, in the roundtail chub population.

Table 5 shows frequency of occurrence and mean numbers of a cestode parasite in the foregut of all cyprinids occurring in Virgin River near Beaver Dam Wash, Arizona, in 1979. This cestode was later identified as *Bothriocephalus acheilognathi*. It is evident that frequency of infections varies seasonally and that the roundtail chub is more frequently infected with more tapeworms per fish than are other native species. The introduced red shiner appears to be about as heavily infected as is the roundtail chub. Table 5 also demonstrates that frequency and density of infection tends to increase in all species in September and December.

Table 6 shows that woundfin in the disturbed river segment near Mesquite tend to be more heavily parasitized throughout the year than at Beaver Dam Wash. The red shiner is heavily parasitized by cestodes at both Mesquite and Beaver Dam Wash, but until 1985 remained abundant throughout the year only near Mesquite.

Thirty-seven adult Asian tapeworms were identified from 24 (27%) of 88 red shiners collected in Virgin River near Mesquite, Nevada, on 25 August 1985. Mesquite, like Twin Bridges and Santa Clara inflow, is in a disturbed segment of the Virgin River.

COMMENTS FOR SELECTED PARASITES OBSERVED DURING STUDY

Posthodiplostomum minimum

This was the most common parasite observed in fishes from the Virgin River in Utah. An excellent review article of North American studies of this fish parasite is found in Spall and Summerfelt (1969b). Metacercariae of the strigeid fluke, *Posthodiplostomum minimum* (MacCallum 1921), the white grub, are reported in most American helminthological surveys of fishes. The metacercaria was first reported over a century ago. It is enzootic in the U.S. exclusive of alpine regions and occurs in abundance in many of the 100 species of North American fishes that have been studied to date (Hoffman 1967). The trematode larvae are generally so numerous in the liver, kidney, heart, and other viscera that many

TABLE 3. Results of parasite inventory for other fish species examined from Twin Bridges, 27–28 July (1–12) and 23 August (13–15) 1985.

Species	Fish number	Measurements (mm) TL	SL	Parasites
Flannelmouth Sucker (*Catostomus latipinnis*)	1	115	90	No parasites
Virgin River Roundtail Chub (*Gila robusta seminuda*)	1	160	145	Metacercariae: *Posthodiplostomum*
	2	145	130	Metacercariae: *Posthodiplostomum*
	3	152	139	Metacercariae: *Posthodiplostomum* Asian Tapeworm: *Bothriocephalus*
	4	155	141	Metacercariae: *Posthodiplostomum* Asian Tapeworm: *Bothriocephalus* Anchor worm: *Laernea*
	5	142	130	Metacercariae: *Posthodiplostomum*
	6	136	123	Metacercariae: *Posthodiplostomum*
	7	134	124	Metacercariae: *Posthodiplostomum*
	8	145	132	Metacercariae: *Posthodiplostomum*
	9	135	126	Metacercariae: *Posthodiplostomum*
	10	125	115	Metacercariae: *Posthodiplostomum*
	11	160	145	Metacercariae: *Posthodiplostomum*
	12	145	130	Metacercariae: *Posthodiplostomum*
	13	170	142	Metacercariae: *Posthodiplostomum*
	14	170	138	Metacercariae: *Posthodiplostomum*
	15	135	112	Metacercariae: *Posthodiplostomum*

TABLE 4. Results of parasite inventory for other fish species examined from mainstream Virgin River about 1/4 mile below inflow of Santa Clara River, 27–28 July 1985.

Species	Fish number	Measurements (mm) TL	SL	Parasites
Flannelmouth Sucker (*Catostomus latipinnis*)	1	115	90	No parasites
	2	164	140	No parasites
Largemouth Bass (*Micropterus salmoides*)	1	58	50	Metacercariae: *Posthodiplostomum*
	2	54	47	Metacercariae: *Posthodiplostomum*
Virgin River Roundtail Chub (*Gila robusta seminuda*)	1	155	145	Metacercariae: *Posthodiplostomum* Asian Tapeworm: *Bothriocephalus*
	2	165	146	Metacercariae: *Posthodiplostomum*

TABLE 5. Frequency of occurrence (%) and mean number of the cestode, *Bothriocephalus acheilognathi*, (Order: Pseudophyllidea) from the foreguts of fishes collected from the Virgin River near Beaver Dam Wash, Arizona, 1979. Abbreviations are as follows: R = *Rhinichtnys osculus;* G = *Gila robusta;* L = *Lepidomeda;* P = *Plagopterus;* N = *Notropis lutrensis.*

Month		R	G	L	P	N	F. Ratio
February	N	28	20	24	22		
	%	3.7	35.0	4.1	0.0	ND	
	Mean	0.3	0.6	0.04	0.0		8.18*
	SE	0.1	0.2	0.1			
June	N	27	4		26		
	%	0.0	25.0	ND	0.0	ND	
	Mean	0.0	0.8		0.0		
	SE	0.0	0.8				
September	N	29	31	31	28	26	
	%	18.2	66.6	12.0	10.7	84.6	
	Mean	0.5	2.0	0.2	0.1	3.9	28.04*
	SE	0.2	0.5	0.2	0.1	0.6	
December	N	23	9	27	27	27	
	%	52.0	88.8	7.4	33.0	88.8	
	Mean	2.2	16.8	1.7	0.6	9.3	23.14*
	SE	1.2	6.0	1.7	0.3	2.0	

Note: Asterisks denote a significant difference among species at $p < 0.01$.
ND = No data.
SE is the standard error of the mean.

TABLE 6. Frequency of occurrence (%) and mean number of cestode parasites (Order: Pseudophyllidea) from the foreguts of fishes from the Virgin River in Nevada, 1979. An asterisk denotes a significant difference between species at $p < 0.01$.

Month		*Plagopterus argentissimus*	*Notropis lutrensis*	t
February	N	24	48	
	%	33	69	
	Mean	0.54	2.94	3.94*
June	N	23	25	
	%	13	36	
	Mean	0.13	3.76	2.01
September	N	34	29	
	%	53	86	
	Mean	1.76	6.03	3.45*
December	N	27	27	
	%	37	81	
	Mean	0.63	6.59	5.07*

observers have implicated them as being histopathogenic. The pathogenicity of the larval stage is usually due to compression or occlusion of a vital organ.

Early literature concerning the classification of *Posthodiplostomum minimum* is invested with synonymy and misinformation, partly because of inadequate description and erroneous identification and partly because some larval stages were described before their life histories, especially the adult, were known. Nomenclatural history has been reviewed by Miller (1954), Hoffman (1958), and Bedinger and Meade (1967).

Studies by Hunter (1937) on the transformation of *Cercaria multicellulata* to *Neascus van cleavei* and by Ferguson (1938) on transformation of metacercariae of *N. van cleavei* to adult *Neodiplostomum* culminated in the first description of the life cycle of *Posthodiplostomum minimum.*

Metacercariae have been found in all visceral organs but occur in abundance in the liver, spleen, kidneys, mesenteries, sinus venosus, heart, and ovaries (Figs. 2a, 2b, and 3a, 3b). Some strigeid larvae show positive histotropic effects toward specific fish tissue in vitro (Davis 1936). Avault and Allison (1965) found that the heart, liver, and kidneys contained approximately 79% of the total metacercariae in bluegill (*Lepomis machrochirus*). Metacercariae have not been reported in fish testis, apparently the only visceral organ alien to this parasite.

The occurrence of numerous metacercariae in visceral organs suggests deleterious effects on the well-being of the host and implicates *P. minimum* as a cause of mortality or morbidity. Hunter (1937, 1940) stated that death resulted if sufficient liver or other visceral tissue were destroyed by the metacercariae. Hughes (1928) observed bluegill, which had a heavy

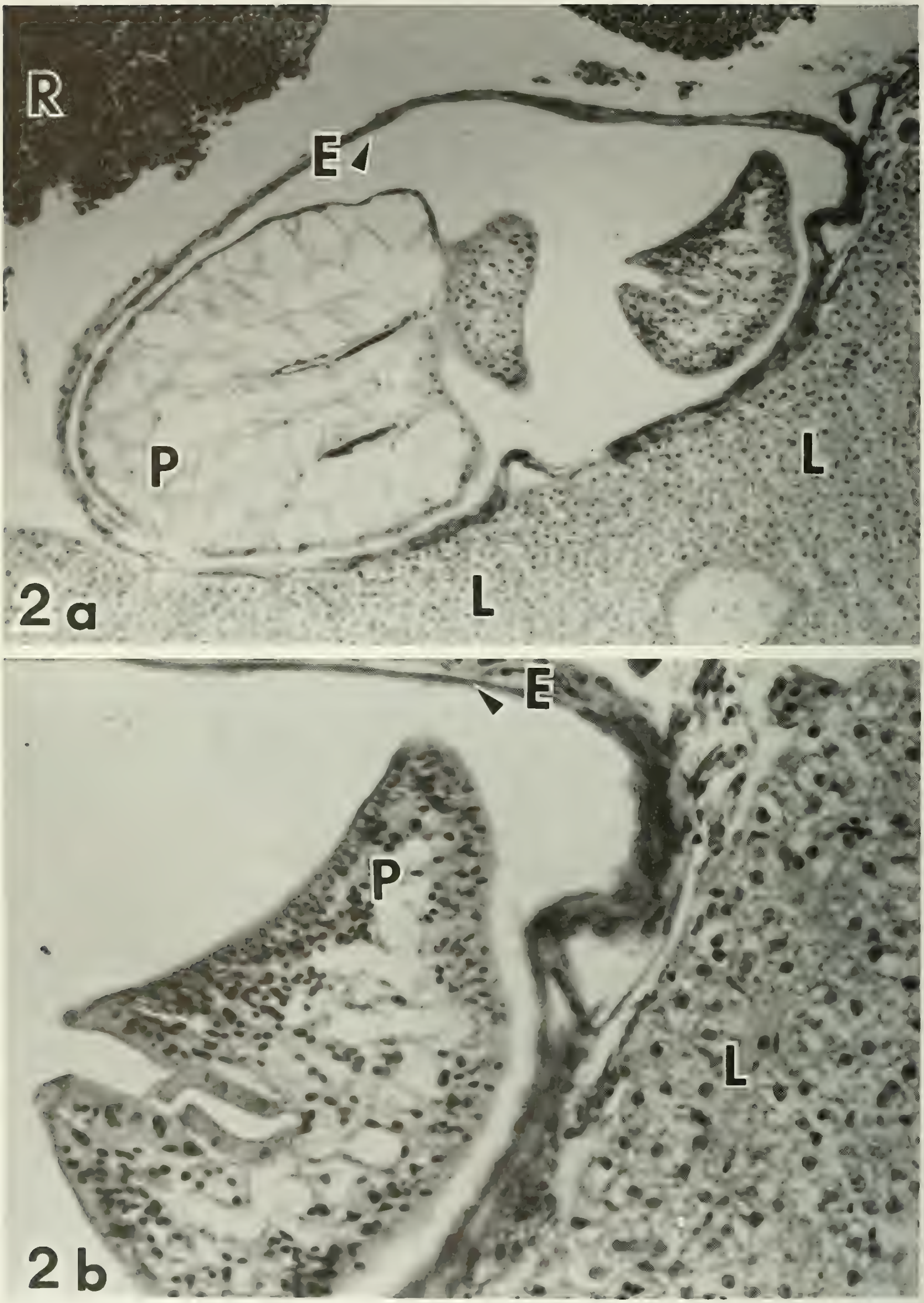

Fig. 2a, b. The metacercarial stage of *Posthodiplostomum minimum* (P) from the internal viscera of *Plagopterus argentissmus*. Note encapsulation (E) of the larval trematode and organ compression of the liver (L). Hemorrhaging (R) has occurred near the site of metacercarial encapsulation. Magnification, 2a—100X, 2b—430X.

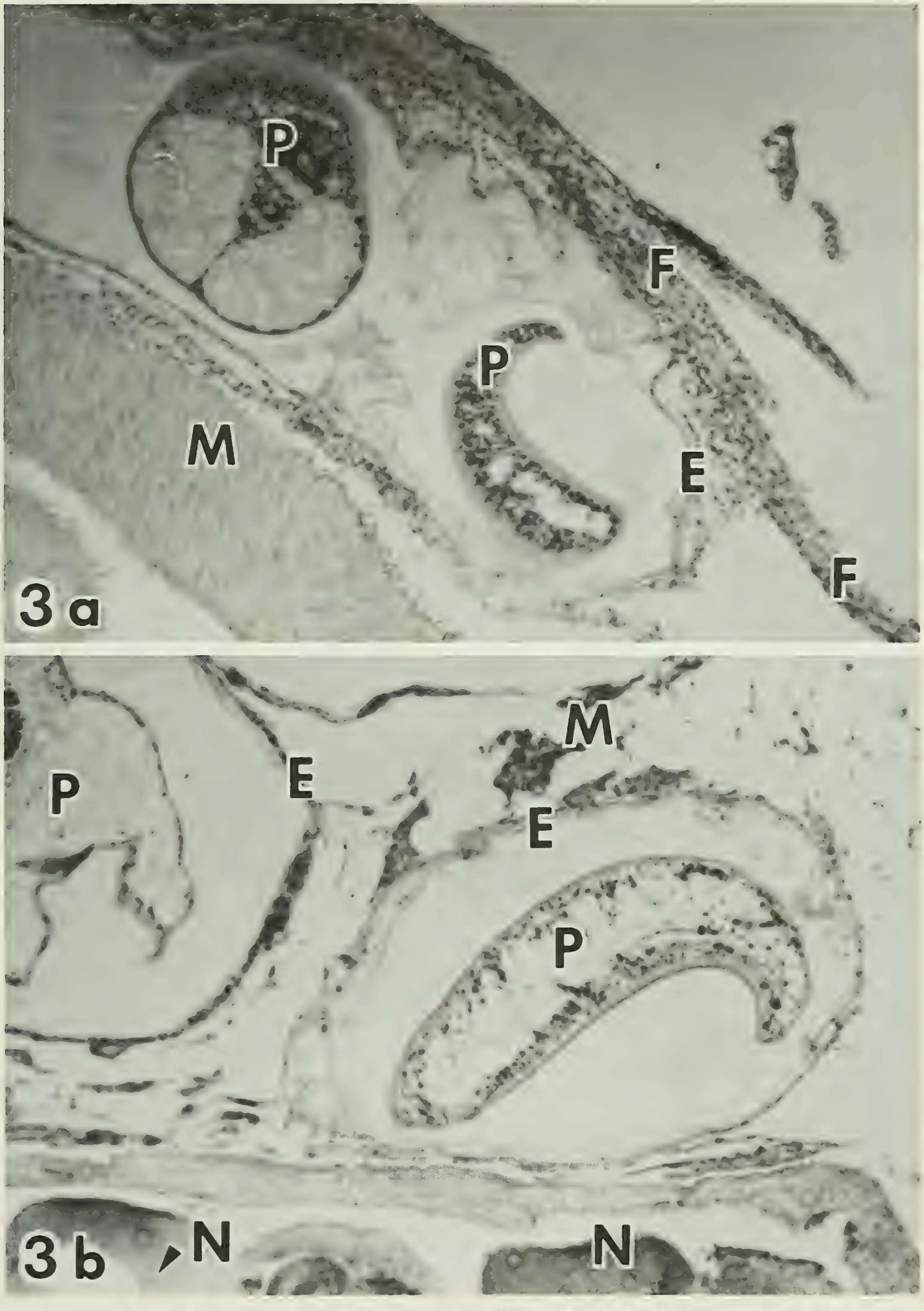

Fig. 3a, b. The larval stage of *Posthodiplostomum minimum* (P) from the internal viscera of *Plagopterus argentissmus*. 3a represents metacercariae encapsulated (E) in outer layer (F) (fibro serosa) of the intestinal tract. Note muscularis externa (M) (100X). 3b represents metacercariae encapsulated (E) in the mesentaries (M) of the viscera exhibiting compression on the intestine (N) (100X).

infection of *P. minimum* metacercariae, in Fife Lake, Michigan, dying in large numbers. This represents an example of a questionable cause-and-effect relationship because the parasite is ubiquitous and usually numerically abundant. More than circumstantial evidence is required to substantiate an allegation of *P. minimum* being a cause for fish mortality. Wild fish, with several hundreds of encysted metacercariae in the liver, sinus venosus, heart, and kidneys, are often observed to suffer no obvious debilitating effects. Colley and Olsen (1963) found as many as 991 metacercariae per bluegil, with metacercariae so dense as to be clumped en masse. Spall and Summerfelt (1969a) have observed 2,041 metacercariae in a bluegill from an Oklahoma reservoir.

Mortality due to stress and trauma from penetration of the cercariae has been observed in the laboratory following exposure of suitable host fish to high numbers of cercariae (Hunter 1937, Bedinger and Meade 1967). Host reactions following cercarial penetration include petechial hemorrhage at the site of invasion followed by congestion of surrounding venules and local edema, and an aggregation of leucocytes at the point of entry, particularly the phagocytic elements. Pathological effects include increased rate of excretion, increased plasma globulin and albumin, increased liver respiration, and decreased hematocrits (Smitherman 1964). Hemorrhage or a decrease in erythropoiesis would reduce hematocrits. The increase in the plasma proteins may represent a homeostatic response to the nutritional demands of the parasite, altered liver function, or effects on capillary permeability.

After encystment (19 days), mortality infrequently occurs. There is no experimental evidence to indicate mortality or other detrimental effects from the occurrence of encysted metacercariae.

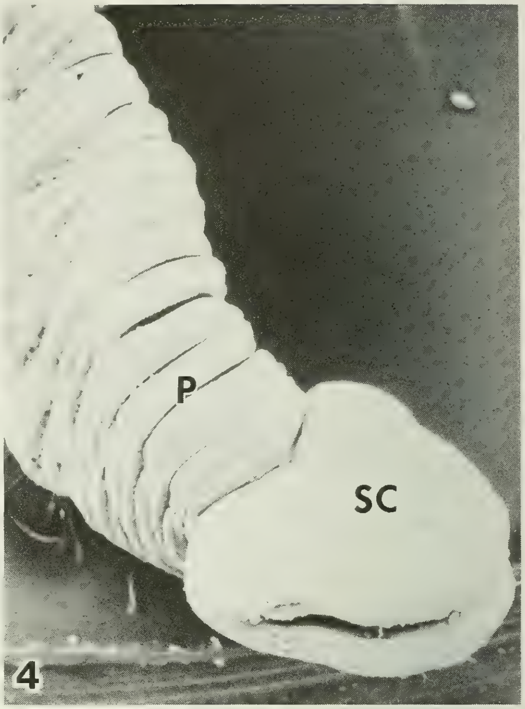

Fig. 4. A scanning electron micrograph of the Asian fish tapeworm, *Bothriocephalus acheilognathi,* from the intestine of the Virgin River roundtail chub, *Gila robusta seminuda.* Note the pit-viper shaped scolex (SC) and numerous proglottids (P). Photographed at 100X magnification.

Bothriocephalus acheilognathi =
(B. gowkongenesis =
B. opsalichthydes)

The Asian fish tapeworm, *Bothriocephalus acheilognathi,* represents a new introduction in North America, brought in through imports of grass carp to this country from China. Because of the new introduction and size of the adult worm, this parasite has become of major concern to fish and game officials throughout the country. Excellent reviews of the histopathology, biology, life history, control, and management of *Bothriocephalus* are found in a series of papers by Nakajima and Egusa (1947a, b, c, 1976a, b).

The Asian fish tapeworm, characterized by its arrow or heart-shaped scolex (Fig. 4), has been a dangerous parasite for cultured grass carp and German carp fingerlings in Europe (Bauer et al. 1981). In Europe it has also been found in European catfish, guppies, mosquito fish, and other species (Hoffman 1983, Hoffman and Shubert 1984). In the United States it has been found in golden shiners and fathead minnows (Hoffman 1976), as well as in grass carp, Colorado squawfish, and mosquito fish. We add speckled dace, roundtail chub, Virgin spinedace, woundfin, and red shiner to that list.

The best known carp parasite transported to the fish ponds of many countries with the

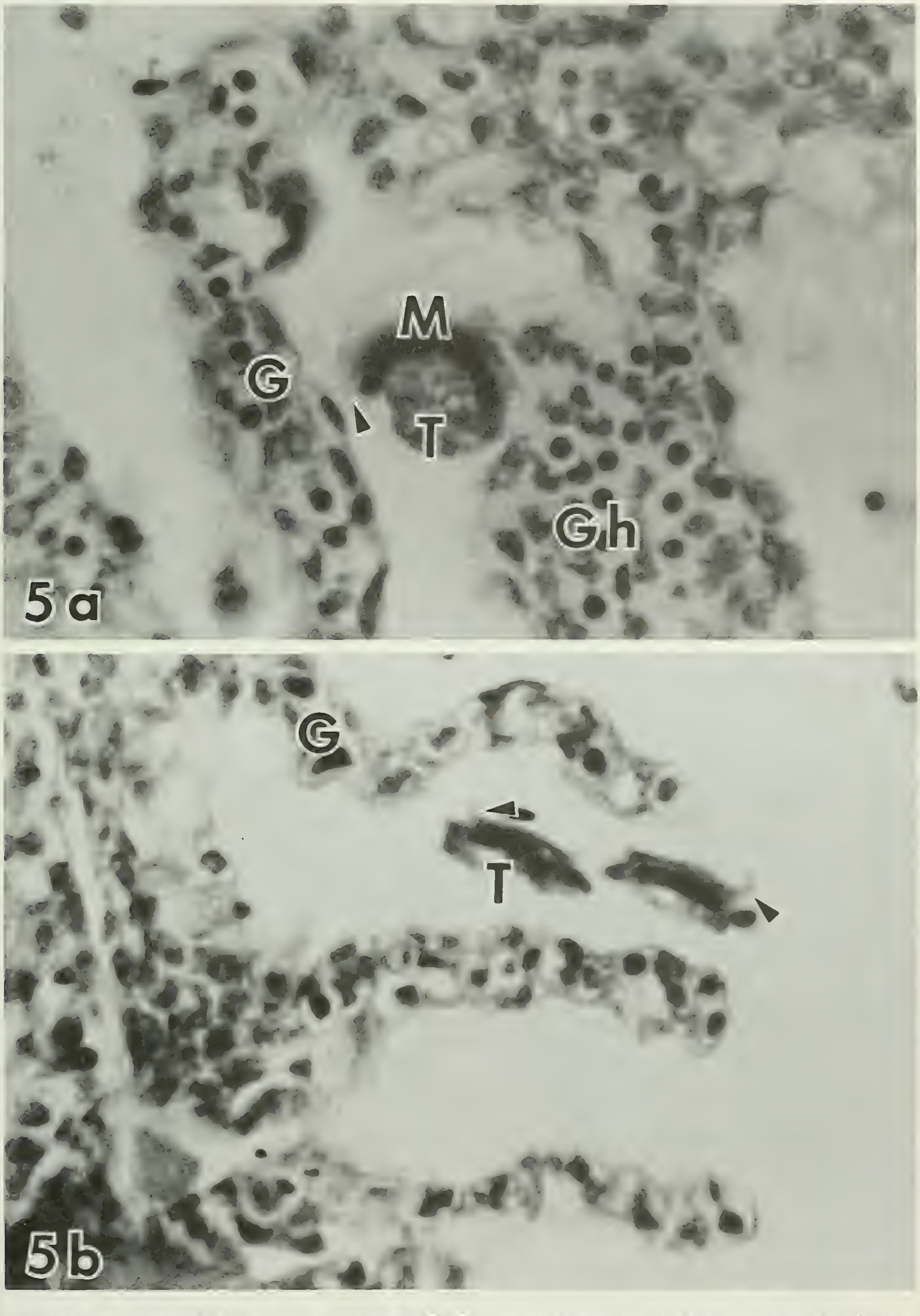

Fig. 5a, b. *Trichodina* (T) infesting the gill lamellae (G) of *Plagopterus argentissmus*. Note the macronucleus (M) and cilia (arrow) characteristic of this ciliate. There is tissue granulation and hypertrophy (gh) of the host gill tissue near one parasite. 1000X magnification.

Chinese carp is *Bothriocephalus acheilognathi* (= *B. gowkongensis*, = *B. opsalichthydis*) (Bauer et al. 1981). All European countries that culture carp in large quantities now have this pathogen. The spread of this parasite to new localities usually results in heavy infection of young fishes during the first years after it appears. *Bothriocephalus acheilognathi*, a thermophyllic parasite, can infect many fish species. Presumably it traveled to the United States by airplane in grass carp shipped from Asia.

Trichodina: Trichodinosis

This is a ciliated protozoan that was commonly observed on the gills of the woundfin minnow in August (Table 2).

This ciliate is ubiquitous among fish parasites throughout the world and usually is of minor concern for fish health. Members of the genus *Trichodina* Ehrenbert (Family; Urceolariidae Stein) are commonly seen on all kinds of aquatic animals. In fish they may settle on the skin in such numbers as to obscure the normal structure (Fig. 5a, 5b), and they are easily recognized by their similarity to a suction disk. Classification methods have been reviewed by Tripathi (1954). *Trichodina* parasitizes the skin, gills, and urinary bladder of the fish and is found both in freshwater and the sea.

The species of *Trichodina* that occur on North American freshwater fishes have not received the attention that they have in other areas of the world even though they are one of the most important groups of ectoparasites of freshwater fishes. Frequent references to trichodinids parasitizing fish occur in fish culture literature but the species are not named, as in the case for our study. Only Mueller (1937, 1938), David (1947), Lom (1963), Lom and Hoffman (1964), Hoffman (1967), and Wellborn (1967) have made major contributions to the knowledge of the taxonomy and distribution of *Trichodina* of North American freshwater fishes. Because of their small size, supposed lack of specific characters, and difficulty of removal from their hosts, they have been largely ignored.

More than 90 species of *Trichodina* have been described from the skin and gills of marine and freshwater fishes of the world (Hoffman 1967, Wellborn 1967). Many of these were described as new only because they were found on a different host or in another geographic location. In many cases the descriptions were inadequate since the uniform body structure of these ciliates yields few characters for differentiation of the species (Lom 1961, 1970, Mueller 1937). The inexact and insufficient descriptions of most early authors make the identification of many species doubtful. But the recently employed silver-impregnation technique of Klein and Chatton-Lwoff (Corliss 1953) reveals details of the adhesive disk that are important features of trichodinid taxonomy. Padnos and Nigrelli (1942) used the silver-impregnation technique to determine the ciliar patterns of trichodinids. But, according to Lom (1958), Raabe (1950) was the first to employ this technique in the study of the structure of the adhesive disk.

Trichodina rarely give rise to pathological manifestations of disease. It may be sporadically found in living fish, but it will only multiply in moribund and weakened ones. A macronucleus, mironucleus, and numerous food vacuoles are to be seen in the cytoplasm.

In our study we observed *Trichodina* on the gill surface (Fig 5a, 5b) of woundfin minnows in August.

DISCUSSION

Deacon and Hardy (1984) referred to segments of the Virgin River above Washington Diversion and above Mesquite Diversion as relatively undisturbed. Segments of the river below these two diversions were referred to as disturbed largely by irrigation withdrawals. Table 7 demonstrates that mean and minimum flows in May-November were substantially reduced at Bloomington below the Washington Diversion in 1985. Table 8 demonstrates a similar reduction in flow at Riverside, below the Mesquite Diversion in 1979. In addition, water quality in disturbed segments of Virgin River is also reduced, largely as a consequence of its use for agricultural irrigation (Sandberg and Sultz 1985). In June 1985 discharge from a salt spring (Pah Tempe Spring) suddenly increased dramatically, resulting in degradation of water quality throughout the Utah portion of the Virgin River (Table 9). Therefore, our 1979 data clearly contrast parasite loads in fishes ex-

TABLE 7. Provisional mean, maximum, and minimum daily discharge (cfs) of the Virgin River at Hurricane and Bloomington, Utah, in 1985.

	Hurricane			Bloomington		
Month	Mean	Maximum	Minimum	Mean	Maximum	Minimum
January	197	361	150	238	433	198
February	201	266	145	220	301	169
March	270	515	153	276	574	171
April	637	982	330	673	1,050	285
May	229	462	103	202	477	63
June	96.9	179	68	44.2	150	25
July	116	565	78	71.2	481	31
August	86.7	91	78	37.4	49	28
September	79.1	125	73	54	132	32
October	76.7	149	52	91.1	142	73
November	183	696	56	191	808	88
December	171	286	84	198	319	119

TABLE 8. Mean, maximum, and minimum daily discharge (cfs) of the Virgin River at Littlefield, Arizona, and Riverside, Nevada, in 1979.

	Littlefield			Riverside		
Month	Mean	Maximum	Minimum	Mean	Maximum	Minimum
January	200	458	139	257	591	178
February	324	389	256	376	447	279
March	603	2,440	252	656	2,440	280
April	1,262	1,840	760	1,111	1,580	692
May	1,559	2,000	962	1,277	1,580	789
June	390	815	79	213	652	1.2
July	68.9	79	63	1.23	18	0
August	127	637	70	23.3	150	0
September	65.9	68	63	9.37	27	0
October	92.3	128	65	50.3	118	17
November	171	211	137	184	225	138
December	194	219	173	192	242	150

TABLE 9. Specific conductance, Virgin River, pre- and postdevelopment of a dramatic increase of flow from Pah Tempe Springs.

	Predevelopment		Postdevelopment
Location of water sample	Hickman 1984–85	Sandberg and Sultz 1985	Hickman 1985
Pah Tempe Springs	16,000–17,500	12,600–13,000	
Below Pah Tempe	5,900–6,600	850–4,430	9,400–10,900
Below Ash Creek	1,500–1,800	905–3,700	6,500–7,900
Above Quail Creek	1,600–2,100	825–3,140	5,000–8,000
Hurricane Bridge or Berry Springs	1,600–1,900	850–3,120	3,900–5,000
Above wash diversion or at inlet	1,600–1,900	820–3,450	3,900–6,500
Above Twin Bridges or above Fort Pierce Wash	1,700–2,200	890–4,390	4,000–5,000
Below Bloomington	2,000–2,2000	870–4,200	3,900–4,800

posed to nearly natural conditions near Beaver Dam Wash with fishes exposed to reduced flow and water quality near Mesquite. Our 1985 data, though designed to contrast the same environmental conditions in a different segment of Virgin River, have the additional complication of a sudden reduction in water quality throughout the entire Utah segment of the river one to two months prior to the time of our collections. Nevertheless, it is clear that the parasite burden in fishes of Virgin River living in more disturbed habitats is much higher than for the same species living in less disturbed habitats.

Cestodes (*Bothriocephalus acheilognathi*) occurred in all Cyprinids inhabiting the lower mainstream of the Virgin River in Arizona and Nevada in 1979 (Tables 5, 6). The exotic red shiner, *Notropis lutrensis*, was infected more frequently and with a greater number of cestodes per individual than were all native species except the Virgin roundtail chub, *Gila robusta seminuda*. Infection frequency and density were variable seasonally, with heaviest parasite loads in general occurring in fall and winter and lightest parasite loads in summer (Tables 5, 6). The woundfin in the "disturbed" segment of the lower mainstream (Table 6) was more heavily infected than was the population in the "undisturbed" segment (Table 5). The red shiner was equally heavily infected in both river segments (Tables 5, 6).

In 1985 cestodes were not detected in woundfin minnows at any of the four locations sampled in Utah. Since we sampled only during late July and August, it is possible that the absence of cestodes reflects only seasonal variation. Both frequency and density of trematode infection in woundfin, however, are much greater in the lower, more disturbed portion of the river near St. George (Table 2).

The reduced flows near St. George may force fish into slow-flowing pools or ponded waters. The more ponded conditions probably permit the development of dense populations of cercariae that are released by snails, an intermediate host in the trematode life cycle. These same conditions make the fish more vulnerable to piscivorous birds, facilitating completion of the trematode life cycle.

The degraded water quality resulting from agricultural return flows may also increase stress on the fish population, which may manifest itself in an increased parasite load. If this is a significant factor, the increased total dissolved solids from increased flows of Pah Tempe Springs beginning in summer 1985 (Table 9) may result in an increased parasite burden in fishes throughout the Utah portion of the Virgin River.

The discovery of the Asian fish tapeworm, *B. acheilognathi*, in the fish population of the Virgin River is of major concern. The parasite was probably introduced into the U.S. by the grass carp. It is considered to be especially dangerous in Europe, where it was also introduced. W. L. Minckley (personal communication) reports that it is especially damaging to Colorado squawfish at the Dexter National Endemic Fish Hatchery in Deming, New Mexico. The high incidence of infection with large numbers of tapeworms in the endangered roundtail chub near Beaver Dam Wash (Table 5) demonstrates the probability that it is similarly damaging to roundtail chubs. Other native fish species showed lower incidence of infection, but all cyprinids were infected at levels that could severely damage the populations. The exotic red shiner was as susceptible to infection at the roundtail chub.

Of the 17 chubs we examined from the river near St. George in July and August 1985, only 3 (18%) contained Asian fish tapeworms. We suggest that this is most likely a reflection of the fact that the tapeworm is just beginning to establish itself in the Utah segment of the river. The tapeworm probably arrived in the spring of 1984 along with the red shiner, *Notropis lutrensis*, which first appeared in April collections of fish from the Virgin River. Red shiners first became common in the St. George portion of the Virgin River during the summer of 1985. They were one of the most heavily infected species in the lower river in 1979 (Tables 5, 6). Twenty-four of 88 red shiners (27%) collected from the lower Virgin River near Mesquite, Nevada, on 15 August 1985 contained 37 adult Asian tapeworms. The red shiner, an excellent host for the Asian tapeworm, was recently established in the Utah portion of the Virgin River and probably brought the cestode into Utah.

ACKNOWLEDGMENTS

We thank Drs. Glenn Hoffman and Lauritz A. Jensen for the identification of the Asian fish tapeworm. This study was funded by the Utah Division of Wildlife Resources (Randy Radant). James Allen and the Electron Optics staff at Brigham Young University provided space and help for the scanning electron microscopy part of this study.

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NEW SCLEROCACTUS (CACTACEAE) FROM NEVADA

Ken Heil[1] and Stanley L. Welsh[2]

ABSTRACT.—Named as new is *Sclerocactus schlesseri* Heil & Welsh. The taxon is described and its relationships discussed.

During the summer of 1981 a peculiarly adapted population of *Sclerocactus* was discovered by cactus enthusiast Dr. David Schlesser in the southeastern quadrant of Nevada, growing on a peculiar, Tertiary lacustrian deposit. The substrate consists of sandy silts to silty clays and appears on the surface to be somewhat gypsiferous. Vegetation in the region consists of typical salt desert shrub community, with galleta (*Hilaria jamesii*) as the main perennial grass component. The long, ribbonlike, uppermost central spines simulate the leaves of the galleta, and the stems are difficult to discern among the grassy areas between the shrubs.

The plants occur singly or in small clumps. General aspect is that of *Sclerocactus whipplei* in a broad sense, but the stem diameter of the plants examined is not as great (4–8 cm, not 5–15 cm), flowers average smaller (3–4 cm, not 3.5–5 cm long), and the spines are densely pubescent, at least when young. The pubescent spines and characteristic flattened upper central spine approaches the condition found in *S. pubispinus* of the nearby Great Basin. The flowers average larger than in *S. pubispinus* (3–4 cm, not 2.5–3.5 cm) and the upper central spine is longer (3–5.5 cm, not 0.5–3.5 cm). The locality is intermediate between that of *S. pubispinus* and *S. whipplei* var. *roseus* as interpreted by Welsh (1984). A specimen of the latter was taken along the Virgin River west of Bunkerville, Nevada, by N. D. Atwood (7821b BRY) in May 1981. A locality for *S. whipplei* (as *S. parviflorus* var. *intermedius*) is mapped from Iron County in southwestern Utah by Benson (1982).

Although some features of the plant discovered by Dr. Schlesser are intermediate between *S. whipplei* and *S. pubispinus*, there are some features that are evidently unique. The narrow stems suggest a parameter that is not shared by the two close geographical congeners. Because of the discordant as well as intermediate features the plant is named as follows:

***Sclerocactus schlesseri* Heil & Welsh** sp. nov. Persimilis *Sclerocacto whipplei* (Engelm.) Britt. & Rose sed in caulibus angustioribus (4–8 cm nec 5–15 cm), floribus minoribus (3–4 cm nec 3.5–5 cm), et spinis pubescentibus differt, et similis *Sclerocacto pubispino* (Engelm.) L. Benson in floribus majoribus (3–4 cm nec 2.5–3.5 cm) et spinis superioribus centralis differt.

Stems dark green, typically solitary, ellipsoid to obovoid, 3–10 (14) cm tall, 4–6 (8) cm wide; ribs 13; tubercules 12–18 mm wide, 8–10 mm long; areoles woolly, finally glabrate; spines flexible, densely pubescent when young; upper central spine 1, ascending, flat or trigonous, ribbonlike, curved, cartillaginous to bony, pubescent to glabrous, 3–5.5 cm long, 1–2.5 mm wide, reddish brown to white; peripheral central spines 2, ascending, flat, ribbonlike, sometimes hooked, pubescent, 2–3 cm long, 0.5–1 mm wide, black to white; lower central spine 1, ascending, flexible, irregularly hooked, pubescent, 2.5–4.5 cm long, to 1 mm wide, black, gray, tan, or white; radial spines 6–9 (12), flattened, flexible, pubescent, 3–14 mm long, white; flowers apical on upper end of the tubercules near the top of the areoles and above the spines, funnelform, 3–4 cm long, 2–3 cm wide, violet pink; sepaloid perianth parts oblanceolate, finely irregularly toothed apically, mucronate, violet pink with brownish midstripes, 1.5–2 cm long, 6–10 mm wide; petaloid perianth parts oblanceolate, entire or slightly undulate, minutely toothed apically, violet pink, 1.5–2 cm long, 4–5 mm wide, filaments red, anthers yellow; stigma lobes 7–9, light green; fruit dry, barrel shaped, naked or with 1 or 2 scales, 1–1.5 cm long, 9–13 mm wide, red to greenish red, dehiscing by a transverse break in the ovary wall, the perianth persistent; seeds 2 mm long (hilum to point opposite), 3 mm wide, ca 1 mm thick, pyriform with slightly flattened apex, shiny black, papillate, becoming less so near the hilum; hilum elliptic, 1 mm wide.

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TYPE.—USA. Nevada. Lincoln County, Tertiary lacustrian deposit at ca 1,464 m in salt desert shrub-grass community, 16 June 1983, K. Heil s.n. (Holotype BRY; isotype NY).

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NEW SPECIES AND NEW RECORDS OF NORTH AMERICAN *PITYOPHTHORUS* (COLEOPTERA: SCOLYTIDAE) PART VII.

Donald E. Bright[1]

ABSTRACT.—Three species of *Pityophthorus* from Mexico are described: *bravoi* (Mexico), *conscriptus* (Morelos), and *ostryacolens* (Morelos). Additional host or locality data are given for: *atomus, corruptus, deletus, diglyphyus, elimatus, exquisitus, furnissi, hylocuroides, molestus, montezumae, nebulosus, nocturnus*, and *vespertinus*. Existing keys are modified to contain all newly described species.

This is the final contribution to a series of papers describing the unnamed species and giving new data for the species of *Pityophthorus* collected by T. H. Atkinson and his colleagues (Centro de Entomologia y Acarologia, Colegio de Postgraduados, Chapingo, Mexico). Unlike the previous papers of this series (Great Basin Nat. 45: 467–482) in which all the new species in a species group were described together and a new key written for the species of the group, each of the species described here is the only new one in a species group. Therefore, only the key couplets from my 1981 monograph (Ent. Soc. Canada Mem. 118) are modified to accommodate the new forms.

Once again I wish to thank Dr. T. H. Atkinson for sending the specimens to me and also thank him and his colleagues for their persistence in searching for Scolytidae in numerous different host plants. I also thank my colleagues Dr. E. C. Becker and Dr. J. M. Campbell for reviewing the manuscript of this paper.

Pityophthorus bravoi, n. sp.

Length 1.9–2.2 mm, 2.7 times longer than wide.

FEMALE.—Frons flattened on a semicircular area extending laterally from eye to eye and from epistoma to well above upper level of eyes; surface shining, with numerous fine punctures and with sparse, erect setae, these more abundant, longer, incurved on periphery. Antennal club broadly oval, 1.4 times longer than wide, widest through segments 2 and 3; suture 1 weakly arcuate, suture 2 more strongly arcuate; segment 1 slightly narrower than 2; first two segments occupy half of total club length. Pronotum less than 1.1 times longer than wide, widest behind summit; sides weakly arcuate; asperities on anterior slope small, scattered, isolated; summit strongly elevated; posterior area of disc distinctly punctured, punctures small, deep, close, surface between punctures moderately shining, finely, minutely reticulate; median line not elevated, impunctate. Elytra 2.0 times longer than wide; apex broadly rounded; discal striae punctured in regular rows, punctures larger, deeper than those on posterior portion of pronotum; discal interstriae only slightly wider than striae or as wide as striae, moderately shining, surface finely, minutely reticulate, interstriae 1, 3, 5, 7 each with a median row of sparse punctures and setae, punctures smaller than those in striae, setae longer than those in striae. Declivity convex, weakly bisulcate; interstriae 2 weakly impressed below 1 and 3, equal in width to discal width, surface as on disc; interstriae 1 very weakly impressed below level of 3, with median row of very small granules and setae; interstriae 3 bearing median row of granules, these slightly larger than those in interstriae 1 and with several long, stout setae (sometimes abraded); punctures in striae 1 and 2 much smaller than those on disc, barely visible.

MALE.—Frons convex, median longitudinal carina weakly elevated from epistoma to upper level of eyes, surface on each side of carina shining, densely, finely punctured, setae absent except along epistomal margin. Pronotum and elytra essentially as described for female except pronotal asperities somewhat stronger and pronotal and elytral punctures larger, deeper. Declivity as in female.

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TYPE MATERIAL.—The holotype (♀) is labeled: "Carr. Mex. Popo, Km. 85, VIII-26-1961, Col. H. Bravo M." /♀/ "HOLOTYPE Pityophthorus bravoi D. E. Bright, 1986, CNC No. 18719." The allotype and 6 paratypes bear the same data.

The holotype, allotype, and two paratypes are in the CNC; four paratypes have been returned to T. H. Atkinson.

COMMENTS.—Adults of this species closely resemble those of *P. clivus* Bright. They differ from those of *P. clivus* by the longer, more obscure carina on the male frons, by the more evenly pubescent female frons, by the slightly more deeply sulcate elytral declivity on which interstriae 2 is not wider than the discal width, and by the slightly larger size.

The key to the species in the Blaudus group (pp. 238–241) in my 1981 monograph should be modified as follows:

(Males)

5. Occurs in Mexico; carina on frons moderately or weakly elevated 6

— Occurs in western United States and western Canada; carina on frons variable in height 6a

6. Carina on frons distinctly, moderately elevated, short, extending to well below upper margin of eyes; 1.7–2.0 mm; Nuevo León ...... *clivus* Bright

— Carina on frons weakly elevated, extending to well above upper margin of eyes; 1.9–2.2 mm; Mexico .... *bravoi* Bright

6a. continue from couplet 6 in monograph.

(Females)

27. Occurs in Mexico; setae on frons sparse; median pair of serrations on anterior pronotal margin longer than others; interstriae 2 equal to or only slightly wider on declivity than on disc 28

— Occurs in western United States and western Canada; setae on frons abundant over entire surface; median pair of serrations on anterior pronotal margin not especially longer than others; interstriae 2 distinctly wider on declivity than on disc .... *sierraensis* Bright

28. Setae on frons absent or very sparse on small area in center; interstriae 2 slightly wider on declivity than on disc; 1.7–2.0 mm; Nuevo León .... *clivus* Bright

— Setae on frons sparse, evenly distributed over surface; interstriae 2 equal in width on declivity and disc; 1.9–2.2 mm; Mexico ...... *bravoi* Bright

29. continue as in couplet 28 in monograph.

Pityophthorus conscriptus, n. sp.

Length 1.7–1.9 mm, 2.8 times longer than wide; color black with light reddish legs and antennae.

FEMALE.—Frons flattened on a large, semicircular area extending from epistoma to well above upper level of eyes, about half of flattened area above upper level of eyes, rising slightly toward epistoma and with low, median granule on epistoma; surface shining, with fine, dense, scattered punctures and long, erect, yellowish setae, these slightly longer and incurved on periphery, denser along epistoma. Antennal club oval, 1.2–1.3 times longer than wide, widest through segment 2; sutures 1 and 2 transverse, 1 more strongly chitinized; segments 1 and 2 occupy half of total club length. Pronotum 1.1 times longer than wide, widest on posterior half; asperities on anterior slope arranged in a series of irregular concentric rows, the three or four rows behind anterior margin composed of individual, closely placed asperities generally arranged in broken rows, some rows not extending completely from side to side, with occasional isolated asperities between rows, upper rows around summit in form of elongate, elevated costae, these sometimes weakly serrate but not divided to base to form individual asperities, each row extending up to half of distance across pronotum, some rows joining adjacent rows; summit not elevated; posterior area of disc distinctly punctured, punctures moderate in size and depth, separated by distance equal to or less than their diameters; surface between punctures smooth, moderately shining, with numerous impressed points; median line broad, impunctate, not elevated. Elytra 1.8 times longer than wide; apex broadly rounded; discal striae punctured in regular rows, punctures larger, deeper than those on posterior portion of pronotum; interstriae slightly narrower than striae, smooth, more brightly shining than posterior portion of pronotum with scattered fine points or lines. Declivity evenly convex, moderately steep; interstriae 1 moderately elevated, devoid of granules; interstriae 2 flat, slightly broader than discal width; interstriae 3 not elevated, unmodified; surface of all interstriae dull, densely micropunctate; striae 1 narrowly impressed, slightly more strongly so on upper half. Interstriae 1 with a median row of erect setae extending from base to apex; interstriae 3, 5, 7 with median row of similar setae extending from or posterior to midpoint of disc to apex.

MALE.—Frons weakly flattened from epistoma to above upper level of eyes, more distinctly, transversely impressed just above epistoma, slightly convex on upper portions; surface densely, strongly punctured, dull on lower half, shining above, setae short, scattered, longer and more abundant in transverse impressions above epistoma. Pronotum and elytra essentially as on female except punctures on pronotum and in striae slightly larger. Declivity steep, deeply bisulcate; interstriae 1 strongly elevated, broad, with median row of 4 or 5 large, acute granules; interstriae 2 much broader than discal width, smooth, distinctly impressed; interstriae 3 strongly elevated, arcuate, with median row of 4 or 5 acute granules, these smaller than those on interstriae 1; surface and vestiture of interstriae as in female.

TYPE MATERIAL.—The holotype (♀) is labeled: "LA HERRADURA, Mpio, Tepoztlan, Mor.[elos], 10 Jie 1982, 1,750 m, (??)3–127, A. Burgos–E. Saucedo"/"HOLOTYPE *Pityophthorus conscriptus* D. E. Bright, 1986, CNC No. 18720."

The allotype and six paratypes bear the same labels. Some of the letters or numbers on the labels are illegible.

The holotype, allotype, and two paratypes are in the CNC; four paratypes have been returned to T. H. Atkinson.

COMMENTS.—Adults of this species are unique by the presence of broken concentric rows of asperities on the lower slope of the pronotum, by the short concentric, anastomatic rows of elevated costae on the upper slope and around the summit of the pronotum, by the deeply bisulcate elytral declivity that bears distinct granules on interstriae 1 and 3 of the male, and by the evenly sloping, not sulcate, not granulate elytral declivity of the female.

This species does not readily fit into any of the species groups I used in my 1981 monograph. Its declivital characters indicate relationship to *P. guatemalensis*, but its pronotal characters seem distinctly unrelated. Adults of this species differ from those of *P. guatemalensis* by the more deeply impressed male declivity, by the less deeply impresseda female declivity that is devoid of granules on the first and third interstriae, by the characters on the pronotum as described above, by the more extensively pubescent female frons, and by the less strongly convex male frons.

The key to species group (p. 22) in my monograph should be modified as follows:

6. (as in monograph)

— Segment 1 of antennal club nearly equal in width to others, club widest through segment 2 .... 7a

7a. Asperities on lower slope of pronotum arranged in broken, concentric rows, those on upper slope and around summit developed into short, concentric, anastomatic costae; male elytral declivity deeply bisulcate, with acute granules on interstriae 1 and 3; female elytral declivity convex, not sulcate, devoid of granules on interstriae 1 and 3 .... Conscriptus group

— Asperities on anterior slope and around summit arranged in even concentric rows, elevated costae not present; elytral declivity variable, not as above 7

7. Continue as in monograph.

Pityophthorus ostryacolens, n. sp.

Length 2.4–2.5 mm, 2.9 times longer than wide; color reddish brown, legs and antenna light reddish or yellowish brown.

FEMALE.—Frons weakly convex, with a smooth, broad, weakly elevated, longitudinal, median elevation extending from epistoma to level of upper margin of eyes; surface lateral to and above elevation densely punctured, punctures small, shallow, becoming larger, deeper toward vertex and laterally toward eyes, surface between punctures shining, generally smooth but with a few, scattered minute granules; vestiture moderately abundant, scattered, consisting of downward pointing, moderately long, yellowish setae, these longer, denser along epistomal margin. Antennal club broadly oval, 1.2 times longer than wide, widest through segment 2; sutures 1 and 2 arcuate; segments 1 and 2 occupy about half of total club length. Pronotum 1.1 times longer than wide, widest at middle; sides very weakly arcuate on basal half, broadly rounded to the weakly serrate anterior margin; anterior slope with numerous, scattered, low asperities, these extending laterally to base and onto posterior discal portion; summit not elevated; posterior area of disc deeply punctured, punctures large, separated by a distance less than their diameters, lateral edges of punctures elevated, forming low asperities except in very limited median area, surface between punctures smooth, shining, with minute impressed points; median line not evident. Elytra 1.8 times longer than wide; apex broadly rounded; discal striae punctured in regular rows, punctures large, deeply impressed, each with a very short seta; interstriae about 1.5 times wider than striae, surface moderately shining, with numerous, scattered, impressed points. Declivity evenly convex, sloping: striae and interstriae essentially as on disc except interstriae 1, 3, 5, 7, etc., with a median row of very fine granules and a median row of erect setae and strial punctures slightly less distinct.

MALE.—Identical to female except setae on frons less abundant and less distinct.

TYPE MATERIAL.—The holotype (♀) is labeled: "Cuernavaca, Mor.[elos], 18.III.82, S-396, 2,190 msnm, T. H. Atkinson"/"*Ostrya virginiana* (Ulmaceae)"/"HOLOTYPE Pityophthorus ostryacolens D. E. Bright 1986, CNC No. 18721." The allotype bears the same locality and host label plus an allotype label.

The holotype and allotype are in the CNC.

COMMENTS.—This species belongs in the Alni group and will key out near *P. alnicolens* Wood. Adults differ by their larger size, by the more distinct longitudinal carina on the frons, by the more weakly serrate anterior pronotal margin, and by the different host and distribution.

The key to the species in the Alni group (pp. 92–93) in my 1981 monograph should be modified as follows:

3. Declivital interstriae 2 bearing a median row of stout setae; elytral striae impressed on disc, interstriae convex; lateral areas of pronotum asperate almost to base; pronotum and elytra shining; Veracruz . . . . *alni* Blackman

— Declivital interstriae 2 not bearing a median row of setae; elytral striae not or only weakly impressed; lateral areas of pronotum punctate to subasperate; pronotum and elytra dull to moderately shining 3a

3a. Length 1.8–2.0 mm; longitudinal carina on frons indistinct, faintly elevated; elytral striae not impressed; in *Alnus*, Veracruz . . . . . *alnicolens* Wood

— Length 2.4–2.5 mm; longitudinal carina on frons distinct, weakly elevated; elytral striae weakly impressed; in *Ostrya*, Morelos . . . . *otryacolens* Bright

4. Continue as in monograph.

NEW HOST OR LOCALITY RECORDS

Only locality records that significantly extend the range or represent the first records since the species was described are listed below. All new host records seen are also listed below. Numerous new state records were seen in the material examined; these will be reported later.

Pityophthorus atomus Wood

Pityophthorus atomus Wood, 1964, Great Basin Nat. 24: 61; Bright, 1981, Ent. Soc. Canada Mem. 118: 44; Wood, 1982, Great Basin Nat. Mem. 6: 1137.

This species was previously recorded only from Oaxaca and Veracruz from an unknown shrub. Two series totaling 17 specimens have been seen with the data: "Pachuca, Edo. de Hidalgo, S-463, 21.V.82, 2,400 m, Col. A. Equihua M." (8) and "Jalapa, VERACRUZ, 25.II.84, FANM 143, Col. Felipe A. Noguera"/"Hosp. *Vernonia* sp. (Compositae)."

Pityophthorus corruptus Wood

Pityophthorus corruptus Wood, 1976, Great Basin Nat. 36: 363; Bright, 1981, Ent. Soc. Canada Mem. 118: 68; Wood, 1982, Great Basin Nat. Mem. 6: 1133.

Known only from the type locality in Puebla from *Toxicodendron* (or *Rhus* sp.). Twenty-nine specimens have been seen with the data: "San Rafael, Mex.[ico], 4.IX.81, S-242, 2,400 m, Atkinson-Equihua"/"Hosp.: *Rhus* sp."

Pityophthorus deletus LeConte

Pityophthorus deletus LeConte, 1879, Bull. U.S. Geol. Geog. Survey 5(3): 519; Bright, 1981, Ent. Soc. Canada Mem. 118: 110; Wood, 1982, Great Basin Nat. Mem. 6: 1040.

This name includes a presently unresolved complex of one or more very closely related and variable species. Seven names (sensu Bright) or six names (sensu Wood) are included as synonyms under the above name.

This species is known from California to South Dakota, south to Durango and Coahuila, Mexico. Five specimens which I have assigned to this species complex have been seen with the labels: (3) "Cerro Tlaloc, Tequesquinahuac, Edo. Mex.[ico], 22.I.80; 3,400 msnm, Col. T. H. Atkinson"/"Hosp.: *Pinus hartwegii* (Pinaceae)" and (2) "Zoquiapan, Edo. Mex.[ico], Altitud: 3,600 msnm, Fecha: 25-III-81, Col. A. Equihua M."/"Hosp. *Pinus hartwegii* (Pinaceae)."

Pityophthorus diglyphus Blandford

Pityophthorus diglyphus Blandford 1904, Biol. Cent.-Amer. 4(6): 240; Bright, 1981, Ent. Soc. Canada Mem. 118: 121; Wood, 1982, Great Basin Nat. Mem. 6: 1058.

Previously known only from Guatemala. Three specimens, all females, were seen with the labels: "Volcan Chichinautzin, Morelos, 30. Jie (?), 1982, 2,790 m, 73–133, J. Burgos"/ "(Pinaceae) *Pinus* sp."

These three specimens could possibly be considered examples of *P. leiophyllae* Blackman based on morphological similarity and locality. The presence of long setae on the third declivital interstriae place it in *P. diglyphus* as presently understood. The two names may be synonyms, but more specimens are needed before a definite conclusion can be made.

Pityophthorus elimatus Bright

Pityophthorus elimatus Bright, 1976, Great Basin Nat. 36: 432; Bright, 1981, Ent. Soc. Canada Mem. 118: 196; Wood, 1982, Great Basin Nat. Mem. 6: 1086.

This species was previously known only from the type locality in Oaxaca. Eight specimens have been seen with the data: "Parque Nal. Zoquiapan, Edo. de Mexico, 3,200 msnm, 24.V.80, S-099, Col. D. Cibrian Tovar."

Pityophthorus exquisitus (Blackman)

Neodryocoetes exquisitus Blackman, 1942, Proc. U.S. Nat. Mus. 92(3147): 196.

Pityophthorus exquisitus: Bright, 1981, Ent. Soc. Canada Mem. 118: 102; Wood, 1982, Great Basin Nat. Mem. 6: 1026.

Pityophthorus inceptis Wood, 1975, Great Basin Nat. 35: 396; Bright, 1981, Ent. Soc. Canada Mem. 118: 102.

This species was previously known from Jalisco and Michoacán. The host is listed as an unknown shrub or in wood crates or wood stems. Four specimens were examined that bore the following labels: "Rancho Tetela, Cuernavaca, Mor[elos], Compositae, 10-Enero-1982, 1,350 m, Col. BUSA-SACE-MAFE."

Pityophthorus furnissi Bright

Pityophthorus furnissi Bright, 1976, Great Basin Nat. 36: 433; Bright, 1981, Ent. Soc. Canada Mem. 118: 144; Wood. 1982, Great Basin Nat. 6: 1094.

Previously known only from the type locality of Amecameca, Mexico. Eight specimens were seen with the following data: "Cerro Tlaloc, Tequesquinahuac, Edo. Mex[ico], 22.I.80, 3,400 msnm, Col. T. H. Atkinson"/ "Hosp.: *Pinus hartwegii* (Pinaceae)."

Pityophthorus hylocuroides Wood

Pityophthorus hylocuroides Wood, 1964, Great Basin Nat. 24: 69; Bright, 1981, Ent. Soc. Canada Mem. 118: 31; Wood, 1982, Great Basin Nat. Mem. 6: 1120.

Previously known only from Hidalgo taken on *Rhus* sp. One specimen has been seen with the data: "Jalapa, VERACRUZ, 21.II.84, FANM 140, Col. Felipe A. Noguera"/"Hosp.: *Tithonia* sp. (Compositae)."

Pityophthorus molestus Wood

Pityophthorus molestus Wood, 1976, Great Basin Nat. 36: 362; Bright, 1981, Ent. Soc. Canada Mem. 118: 61; Wood, 1982, Great Basin Nat. Mem. 6: 1131.

Previously known only from the type locality in San Luis Potosi. Three specimens were seen with the data: "Apulco Centre Zacapoaxtla y Cuetzalan, Pue[bla], 4.V.81, 1,480 m, Col. T. H. Atkinson y A. Equihua, S216"/ "Hosp.: *Liquidambar styraciflua*."

Pityophthorus montezumae Bright

Pityophthorus montezumae Bright, 1978, Great Basin Nat. 38: 81; Bright, 1981, Ent. Soc. Canada Mem. 118: 272; Wood, 1982, Great Basin Nat. Mem. 6: 1079.

Known previously only from the type locality in Chiapas. Two specimens have been seen with the data: "Parque Nal. Zoquiapan, Edo. de Mexico, 3,200 msnm, 24.V.80, S-099, Col. D. Cibrian Tovar" (1) and "Parque Nal. Zoquiapan, Edo. Mexico. Agosto 79, Hos. *Pinus hartwegii*. T. H. Atkinson" (1).

Pityophthorus nebulosus Wood

Pityophthorus nebulosus Wood, 1976, Great Basin Nat. 36: 363; Bright, 1981, Ent. Soc. Canada Mem. 118: 100; Wood, 1982, Great Basin Nat. Mem. 6: 1126.

This species was previously known only from the type series collected at Lake Catemaco, Veracruz from *Bursera* sp. A series of 10 specimens was seen bearing the labels: "Campo Exptal. I.N.I.F., Escarcega, CAMP[ECHE], 14.IX.83, AEV. 51, Col. A. Estrada V."/"*Bursera semaruba* (Burseraceae)."

Pityophthorus nocturnus Schedl

Pityophthorus nocturnus Schedl, 1938, Archiv Naturgesch. 7: 185; Bright, 1981, Ent. Soc. Canada Mem. 118: 192; Wood, 1982, Great Basin Nat. Mem. 6: 1087.

Pityophthorus hidalgoensis Blackman, 1942, Proc. U.S. Nat. Mus. 92: 215.

This species was previously known from the states of Chiapas, Hidalgo, and Veracruz in Mexico and from Guatemala and Honduras. Three series have been seen with the lables: "Taxco, Guerrero, 22-II-82, S-325, 1,900 m, Col . Atkinson y Equihua"/"Hosp. *Pinus* sp."; "La Herradura, Cuernavaca, Mor.[elos], 10 Diciembre 1982, 1,810 m, SM-104, E. Saucedo-A. Burgos"/"(Pinaceae, *Pinus* sp." and "Acajete, Ver.[acruz]), 22-XI-83, FAMN 91, Col. Felipe A. Noguera"/"Hosp. *Pinus patula* (Pinaceae)."

Pityophthorus vespertinus Bright

Pityophthorus vespertinus Bright, 1978, Great Basin Nat. 38: 83; Bright, 1981, Ent. Soc. Canada Mem. 118: 119; Wood, 1982, Great Basin Nat. Mem. 6: 1058.

This species was previously known from only four specimens collected from *Pinus* sp. in Durango. Six specimens that are referred to this species have been seen bearing the labels: "Acajete, Ver[acruz], 22-XI-83, FANM 91, Col. Felipe A. Noguera"/"Hosp. *Pinus patula* (Pinaceae)."

EFFECTS OF DWARF MISTLETOE ON SPRUCE IN THE WHITE MOUNTAINS, ARIZONA

Robert L. Mathiasen[1], Frank G. Hawksworth[2], and Carleton B. Edminster[2]

Abstract.—Mortality of spruce in mixed conifer stands moderately to heavily infested with western spruce dwarf mistletoe was two to five times greater than in healthy stands in the White Mountains, Arizona. Ten-year volume growth loss for heavily infected spruce trees ranged from 25% to 40%. Estimates of growth loss for spruce on a stand basis ranged from 10% to 20% in heavily infested stands. Because western spruce dwarf mistletoe is prevalent in the White Mountains and causes increased mortality and reduced growth, its control should be included in management of mixed conifer stands there.

Western spruce dwarf mistletoe (*Arceuthobium microcarpum* [Engelm.] Hawksw. & Wiens) is a damaging parasite of Engelmann spruce (*Picea engelmannii* Parry), blue spruce (*P. pungens* Engelm.), and bristlecone pine (*Pinus aristata* Engelm.) in the southwestern United States (Hawksworth and Wiens 1972, Mathiasen and Hawksworth 1980). The distribution of western spruce dwarf mistletoe is confined to Arizona (Pinaleno and White Mountains, San Francisco Peaks, Kendrick Peak, and the North Rim of Grand Canyon) and New Mexico (Mogollon and Sacramento Mountains) (Hawksworth and Wiens 1972, Mathiasen and Jones 1983). Western spruce dwarf mistletoe is most prevalent in the White Mountains, Arizona (Apache-Sitgreaves National Forest), where it has been reported to be in over 60% of the spruce type and is a primary factor associated with spruce mortality (Hawksworth and Graham 1963). It is more common in the lower mixed conifer forests than in spruce-fir forests, possibly because its distribution is restricted to below approximately 10,400 feet (Acciavatti and Weiss 1974, Mathiasen and Hawksworth 1980).

Gottfried and Embry (1977) reported blue spruce was more heavily infected than Engelmann spruce in a virgin mixed conifer stand in the White Mountains, Arizona, but overall infection of both species was relatively low (2% and 5% for Engelmann and blue spruce, respectively). However, Gottfried and Embry also reported that almost 20% of their sample points containing blue spruce had infected trees. Hawksworth and Graham (1963) reported 63%–70% of the spruce stands they surveyed in the White Mountains, Arizona, were infested with western spruce dwarf mistletoe. Our observations in the White Mountains also indicate blue spruce is heavily infected in many mixed conifer stands, particularly along drainages. Jones (1974), Gottfried and Embry (1977), and Ronco et al. (1984) proposed general recommendations for silvicultural management of mixed conifer forests that consider the dwarf mistletoe problem.

Although western spruce dwarf mistletoe represents the most damaging disease agent in southwestern mixed conifer forests dominated by Engelmann or blue spruce, little information is available regarding its effect on mortality and growth of its principal hosts. This study provides additional quantitative data on the mortality and growth loss caused by western spruce dwarf mistletoe in the White Mountains, Arizona.

Methods

In 1981, 99 temporary rectangular plots ranging in size from 0.1 to 0.8 acre were placed in mixed conifer stands with various densities of Engelmann and/or blue spruce in the White Mountains, Arizona (Apache-Sitgreaves National Forest). Two-thirds of the plots were infested with various levels of western spruce dwarf mistletoe. Plots were selected in an attempt to maintain a homogeneous distribution of age classes, species composition, and dwarf mistletoe infection. Plots were only located in stands that had not been disturbed for at least 12 years prior to data collection.

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The following data were recorded for each tree greater than 4.5 feet in height in each plot: species, diameter breast height (DBH) to the nearest 0.1 inch, dwarf mistletoe rating (six-class system, Hawksworth 1977)[3], crown class (dominant, co-dominant, intermediate, suppressed), tree condition (live or dead), and ten-year radial wood growth at DBH to the nearest 0.05 inch. Overstory $\overline{\text{DMR}}$ values were calculated using DMR for spruce trees only.

Height and age data were measured as follows: total height to the nearest 1.0 foot for two to three living or dead trees from each one-inch diameter class represented for each species in a plot; height to the base of the live crown to the nearest 1.0 foot for live trees measured for total height; distance from the ground to the tenth whorl from the top of live trees measured for total height; age at DBH for two live trees from each two-inch diameter class represented for each species in a plot. Height versus diameter curves were developed for each plot, and these curves were used to estimate present and past heights for trees with only measured diameters. Present volumes and past ten-year volumes were calculated from diameter and height data for Engelmann and blue spruce using the volume equations for Engelmann spruce developed by Hann and Bare (1978). Ten-year periodic annual volume increment (cubic feet/year) was calculated using present and past volumes for spruces greater than 6.0 inches at DBH.

RESULTS

THE SAMPLE.—Of the 99 plots sampled, 34 were predominantly Engelmann spruce, 42 were predominantly blue spruce, and 23 had approximately equal representation of Engelmann and blue spruce based on stems/acre. Basal areas (square feet/acre) ranged from 10 to 134 for blue spruce and from 6 to 156 for Engelmann spruce. However, approximately one-third of the plots sampled had Engelmann or blue spruce basal areas of less than 50 square feet/acre:

	Number of plots	
Basal area (square feet/acre)	Engelmann spruce	Blue spruce
< 50	31	37
51–100	6	8
>100	5	12

The majority of the plots sampled had spruce densities (stems/acre) of less than 200:

	Number of plots	
Stems/acre	Engelmann spruce	Blue spruce
<100	17	19
101–200	13	21
201–300	5	5
>300	7	12

One-third of the plots had no western spruce dwarf mistletoe infection and the remainder ranged from light to heavy:

$\overline{\text{DMR}}$	Number of plots
0	33
0.1–1.0	27
1.1–2.0	20
2.1–3.0	10
>3.0	9

MORTALITY.—Percent mortality was determined for the following size classes: small saplings (DBH 0.1–1.0 inches), large saplings (DBH 1.1–5.0 inches), poles (DBH 5.1–10.0 inches), small sawtimber (DBH 10.1–16.0), and large sawtimber (DBH greater than 16.0 inches) by 1.0 $\overline{\text{DMR}}$ classes (Table 1). Mortality of small and large saplings was approximately the same for healthy plots ($\overline{\text{DMR}}$ 0) and for plots with a $\overline{\text{DMR}}$ less than 2.0. However, percent mortality for these size classes was approximately two and four times greater than in healthy plots for $\overline{\text{DMR}}$ classes 2.1–3.0 and greater than 3.0, respectively. Mortality of pole size spruce increased rapidly as $\overline{\text{DMR}}$ increased. Mortality of pole-sized Engelmann spruce was higher than for blue spruce in the higher $\overline{\text{DMR}}$ classes ($\overline{\text{DMR}}$ greater than 2.0). This trend was reversed in the small and large sawtimber size classes,

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[3] The six-class dwarf mistletoe rating system divides the live crown of a tree into thirds, and each third is rated separately as: 0, no infected live branches; 1, less than 50% of the live branches infected; 2, more than 50% of the live branches infected. The ratings for each third are totaled to obtain a dwarf mistletoe rating (DMR) for the tree. Adding the DMRs for all live trees in a stand and dividing the total by the number of trees is the average stand dwarf mistletoe rating ($\overline{\text{DMR}}$). The six-class system is a standard method for quantifying the intensity of mistletoe infection for individual trees or stands.

TABLE 1. Percent mortality of Engelmann and blue spruce by 1.0 $\overline{\text{DMR}}$ classes and size classes.

	Size class (Inches)											
$\overline{\text{DMR}}$	Small sapling (0.1–1.0)		Large sapling (1.1–5.0)		Poles (5.1–10.0)		Small sawtimber (10.1–16.0)		Large sawtimber (>16.0)		All trees	
Class	E[1]	B[2]	E	B	E	B	E	B	E	B	E	B
0	5	4	7	9	7	4	9	5	6	4	6	6
0.1–1.0	7	1	5	6	17	10	11	3	2	0	8	4
1.1–2.0	2	3	7	6	18	18	12	23	10	10	10	14
2.1–3.0	10	9	12	16	20	15	17	27	11	20	16	17
>3.0	20	17	32	25	34	24	20	33	19	33	23	28

[1] Engelmann spruce
[2] Blue spruce

TABLE 2. Percentage of dead trees with DMR 2–6 by size class.[1]

Size class (Inches)	Total trees	Dwarf Mistletoe Rating[2] 2	3 (Percent)	4	5	6
Small sapling (0.1–1.0)	20	5	10	20	30	35
Large sapling (1.1–5.0)	63	8	11	14	27	40
Poles (5.1–10.0)	29	0	0	14	28	58
Small sawtimber (10.1–16.0)	33	0	0	6	36	58
Large sawtimber (>16.0)	14	0	0	14	28	58
Total	159	4	6	13	30	47

[1] Includes both Engelmann and blue spruce
[2] Includes only dead trees that could be assigned an accurate DMR

TABLE 3. Mean ten-year periodic annual volume increment for Engelmann and blue spruce greater than 6.0 inches DBH by DMR class.

DMR class	N	Mean ten-year periodic annual volume increment (cubic feet/year)	Percent difference from DMR 0
0	620	0.32 A[1]	—
1	48	0.34 A	+6
2	94	0.31 A	−3
3	127	0.30 A	−6
4	100	0.28 B	−12
5	128	0.24 C	−25
6	107	0.20 D	−38

[1] Numbers followed by different letters are significantly different. Oneway AOV, $\alpha = 0.05$, Student-Newman-Kuels.

where blue spruce had a more rapid increase in mortality as $\overline{\text{DMR}}$ increased. Mortality of small sawtimber was from two to five times greater in the most heavily infested plots than in healthy plots. Mortality of large sawtimber was from three to eight times greater in the most heavily infested plots (Table 1).

Nearly half of the dead spruce that could be accurately assigned a DMR were rated as class 6 trees (Table 2). This was true for all size classes except the small sapling class where approximately one-third of the trees were rated as class 5 or 6. The percentage of dead trees rated as class 4 ranged from 6% for the small sawtimber size class to 20% for the small saplings. Few dead spruce were rated as class 2 or 3 in the sapling size classes, and none were rated 2 or 3 in the pole and sawtimber size classes.

EFFECT ON VOLUME GROWTH.—Mean ten-

TABLE 4. Percent infection of live trees by DMR and 0.5 $\overline{\text{DMR}}$ classes[1].

$\overline{\text{DMR}}$ class	Dwarf mistletoe rating (Percent) 0	1	2	3	4	5	6
0.1–0.5	82	13	4	1	0	0	0
0.6–1.0	50	32	6	8	2	1	1
1.1–1.5	40	25	14	9	5	4	3
1.6–2.0	23	32	17	15	6	4	3
2.1–2.5	16	26	11	19	10	11	7
2.6–3.0	8	19	19	19	9	12	14
3.1–3.5	6	19	12	22	19	14	8
3.6–4.0	2	7	12	22	21	20	16
4.0+	1	6	10	11	20	29	23

[1] All spruce combined

year periodic annual volume increment (cubic feet/year) was determined for all spruce greater than 6.0 inches (DBH) for DMR classes 0-6 (Table 3). The results do not include growth loss due to mortality of individual trees.

INFECTION AND GROWTH LOSS ON A STAND BASIS.—The percentage of live trees infected for both Engelmann and blue spruce by individual tree DMR and by 0.5 $\overline{\text{DMR}}$ classes are presented in Table 4. The percentage of trees in the heaviest infection class (DMR 6) ranged from 0% in $\overline{\text{DMR}}$ class 0.1–0.5 to 23% in $\overline{\text{DMR}}$ class 4.0+. A summary of the percentage of trees in DMR classes 4–6 (those in which significant growth loss occurs) is as follows:

$\overline{\text{DMR}}$ class	Percentage of trees in DMR class 4–6
0.1–0.5	0
0.6–1.0	4
1.1–1.5	12
1.6–2.0	13
2.1–2.5	28
2.6–3.0	35
3.1–3.5	41
3.6–4.0	57
4.0 +	72

Stand growth loss was estimated by the distribution of infected spruce by $\overline{\text{DMR}}$ classes (Table 4), and based on the following estimates of growth loss for individual trees by DMR class (Page 6): DMR 1—0%, DMR 2—0%, DMR 3—5%, DMR 4—10%, DMR 5—25%, DMR 6—40%. Stand growth loss by 1.0 $\overline{\text{DMR}}$ classes based on the above estimates was:

$\overline{\text{DMR}}$ class	Estimated percent loss on a stand basis
0.1–1.0	1
1.1–2.0	3
2.1–3.0	9
3.1–4.0	12
4.0 +	20

DISCUSSION

Mortality of Engelmann and blue spruce in mixed conifer stands moderately to heavily infested with western spruce dwarf mistletoe is from two to five times greater than for healthy stands in the White Mountains, Arizona. Approximately 20% to 35% of the spruce sampled in heavily infested stands were dead, indicating western spruce dwarf mistletoe is a primary factor associated with spruce mortality. Hawksworth and Graham (1963) also reported high mortality rates for spruce in western spruce dwarf mistletoe–infested mixed conifer stands in the White Mountains.

Nearly half of the dead trees that could be accurately assigned dwarf mistletoe ratings were class 6 trees. Approximately one-tenth and one-third of these dead spruce were in DMR class 4 and 5, respectively. This was true for all size classes of spruce except the small sapling size class, where more dead saplings were rated as class 4. The high mortality rate in class 5 trees for spruce contrasts to mortality patterns in dwarf mistletoe-infected pines, where mortality is predominantly in class 6 trees (Hawksworth and Lusher 1956).

Heavy dwarf mistletoe infection (DMR 5-6) severely reduces volume increment of spruce in the White Mountains. Lightly infected spruce (DMR 1-2) do not suffer any detectable growth loss and moderately infected spruce (DMR 3-4) only suffer losses ranging from approximately 5% to 10%. These results are similar to those reported for southwestern dwarf mistletoe (*Arceuthobium vaginatum* subsp. *cryptopodum* [Engelm.] Hawksw. & Wiens) parasitizing ponderosa pine (*Pinus ponderosa* Laws.) in the Southwest (Hawksworth 1961).

Estimates of growth losses on a stand basis ranged from approximately 10% to 20% for heavily infested stands ($\overline{DMR}$ greater than 2.0). Lightly to moderately infested stands are estimated to have losses less than 3%. Our estimates of the effects of western spruce dwarf mistletoe on the growth of spruce are the first reported for this parasite-host combination.

Western spruce dwarf mistletoe is a common parasite of spruce in mixed conifer stands in the White Mountains, Arizona. Because heavy infection by western spruce dwarf mistletoe severely reduces the growth of trees and stands and is associated with increased spruce mortality, silvicultural control of the parasite should be a primary concern of resource managers. Heavily infected spruce should be removed from infested stands whenever possible to reduce the impact of this parasite on forest productivity.

ACKNOWLEDGMENTS

The authors acknowledge the assistance of Mr. David Conklin with the field data collection. This study was conducted as part of a cooperative research project between the USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, and the Department of Plant Pathology, University of Arizona, Tucson, Arizona.

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HYDROLOGY OF BEAR LAKE BASIN AND ITS IMPACT ON THE TROPHIC STATE OF BEAR LAKE, UTAH-IDAHO

Vincent Lamarra[1], Chuck Liff[1], and John Carter[1]

ABSTRACT.—Bear Lake is a large, relatively pristine lake located in a graben valley. The lacustrine environment is more than 35,000 years old. Over that period of time, the Bear River intermittently flowed into Bear Lake. Approximately 10,000 to 8,000 BP, the Bear River ceased flowing directly into the lake. Between 1912 and 1924, channels were dug that diverted Bear River flows into the lake. An analysis was conducted to determine the impacts of Bear River flows upon the hydrologic and nutrient budgets of the Bear Lake ecosystem. In addition, the resulting limnological conditions were evaluated. Based upon eight years of historical data (1976 to 1984), regression relationships were developed that allowed an estimation of the historical conditions in Bear Lake (1923 to present) with and without the influence of the Bear River.

Bear Lake, located on the northern border of Utah, is a 282 km^2 natural body of water. The lake presently occupies most of the southern half of the Bear Lake Valley. The geology of the area was first mapped by Richardson (1913) and Mansfield (1927) and more recently by Armstrong and Cressman (1963), McClurg (1970), and Kaliser (1972). The Bear Lake basin is a graben valley bordered on the east and west by normal faults, with Mesozoic and Cenozoic rocks on the east and Paleozoic, Mesozoic, and Cenozoic rocks on the west. The exact age of the lake is presently unknown; however, stratigraphic studies by Robertson (1978) have verified previous morphologic interpretations by Mansfield (1927), which suggest a glacial age for the origin of Bear Lake. Robertson (1978) suggested the lake has had a continuous lacustrine history of at least 35,000 years (BP). However, unlike pluvial lakes Thatcher and Bonneville, which formed in closed basins and were therefore regulated by climatic fluctuations, the early conditions within the Bear Lake Valley remained opened with a northward drainage along the Bear River.

Over the last 28,000 years, the major water level fluctuations in the Bear Lake Valley have been the result of downcuttings of the northern valley outlet and two periods of faulting within the southern Bear Lake Valley. Early conditions within the lake indicated a widespread bay and marsh ecosystem. Tectonic activity lowered the valley differently, resulting in marshes and shallow bays occupying the northern Bear Lake Valley and a deep lake to the south (Robertson 1978). Current conditions have continued over the last 8,000 years with the present outlet of the Bear River northward along the east side of the valley. During most of this time, the lake has been isolated from the major drainage networks (primarily the Bear River). This has led to the occurrence of four endemic fish species that still inhabit the lake in large numbers, and a unique macrochemistry with magnesium as the predominant cation (Kemmerer et al. 1923).

At the present time, Bear Lake is no longer considered a closed basin. Its isolations ended in 1912 with the development of Stewart Dam, Lifton Station, and the diversion of the Bear River into Dingle Marsh. Although historically the marsh (and therefore the Bear River) was separated from the lake by a naturally occurring sandbar, it now serves as a water storage and transfer facility. Water is diverted from the Bear River into the marsh during spring runoff (March–July) and allowed to flow into Bear Lake. When irrigation demands increase during the summer, water flows into the marsh from Bear Lake and then into the Bear River downstream from the diversion dam.

Previous studies (Nunan 1972) have indicated that the storage of Bear River water has altered the macrochemistry of Bear Lake, reducing the TDS (total dissolved solids) levels

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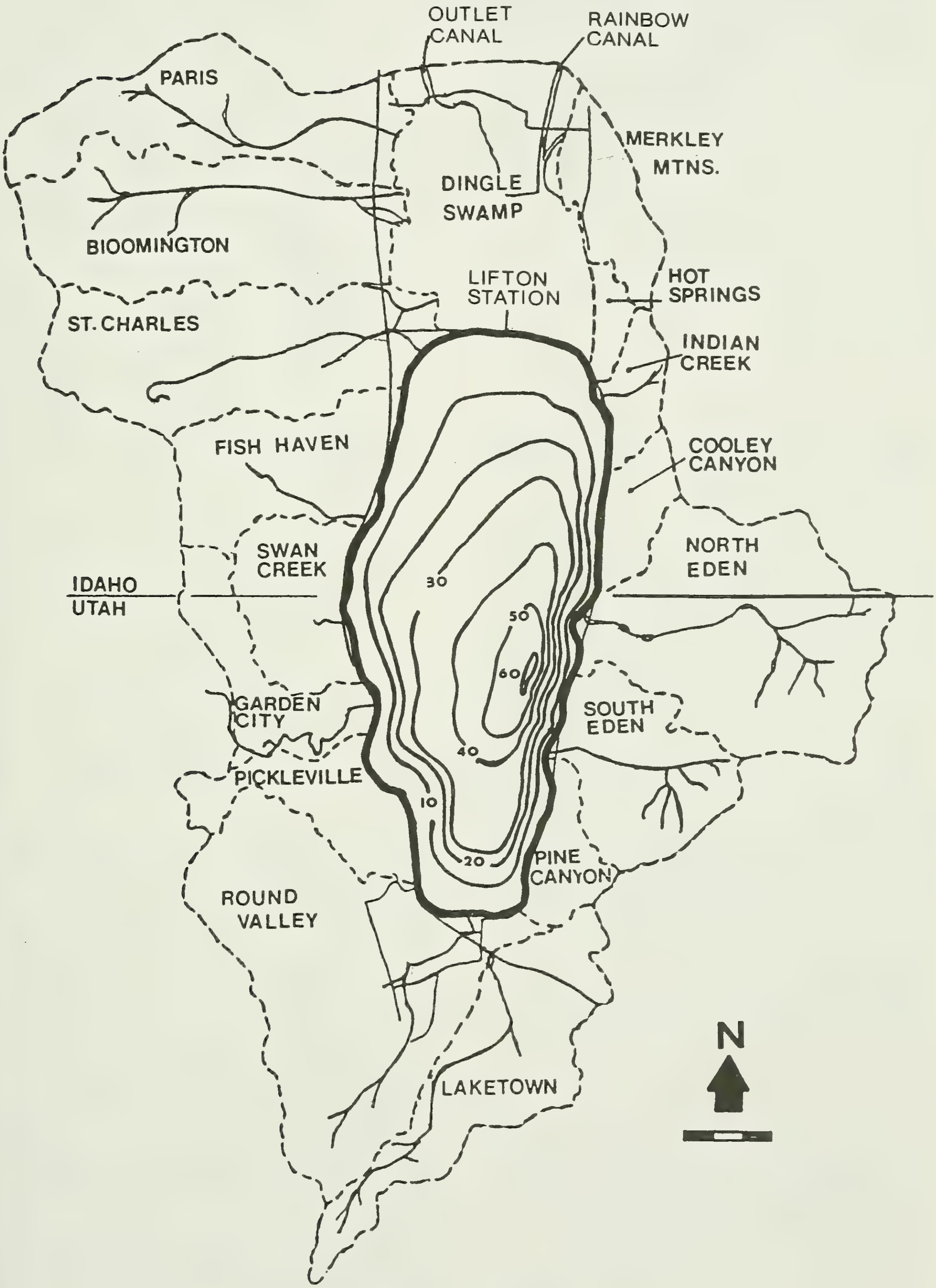
OUTLET CANAL
RAINBOW CANAL
PARIS
MERKLEY MTNS.
DINGLE SWAMP
BIOOMINGTON
LIFTON STATION
HOT SPRINGS
ST. CHARLES
INDIAN CREEK
FISH HAVEN
COOLEY CANYON
SWAN CREEK
NORTH EDEN
IDAHO
UTAH
30
50
60
GARDEN CITY
SOUTH EDEN
40
PICKLEVILLE
10
20
PINE CANYON
ROUND VALLEY
N
LAKETOWN

Fig. 1. Watershed and bathemetric map of Bear Lake, Utah-Idaho. Depth contours are in meters.

from over 1000 mg/l to 500 mg/l during a 50-year period. Recently Lamarra et al. (1984) has noted that the Bear River has also altered the trophic state of Bear Lake. Because of the dominant role of the Bear River in the historical as well as the current hydrological and limnological conditions of Bear Lake, a more detailed description of the impacts upon the lake is needed. It is therefore the purpose of this study to quantitatively describe the current impact of the Bear River upon the hydrology and trophic state of Bear Lake over the last decade and to empirically describe the historical conditions that have existed within the lake during the last 60 years.

METHODS

To distinguish the water quality impacts of the Bear River from the historical Bear Lake watershed, mass nutrient loadings were determined for each major tributary basin and the Bear River (Figs. 1, 2). Water quality analyses (total phosphorus, total nitrogen, total organic carbon, ortho-phosphate, ammonia, nitrate, and nitrite) were performed according to standard methods (APHA 1980). Flow measurements were determined on site or obtained from Utah Power and Light Company.

Water samples were also collected at eight depths at a limnetic site corresponding to the deepest area in Bear Lake (63 m). Analyses included temperature, oxygen, pH, and conductivity in addition to the nutrients previously mentioned. Algal biomass (chlorophyll *a*) was determined by the Fluorometric procedure using a Turner Model III Fluorometer.

Meteorological data were obtained from the NOAA Station at Lifton. Water quality of rain events was previously determined (Herron et al. 1984) and used in this study.

RESULTS

The Bear Lake ecosystem and its associated watersheds cover approximately 8,250 km^2, with 7,000 km^2 in the upper Bear River basin and the remaining 1,250 km^2 within the natural Bear Lake drainage. These major watersheds are within the states of Idaho, Utah, and Wyoming (Fig. 2) and lie within the Great Basin. The results of this study will be presented separately by drainage basin and Bear Lake limnology.

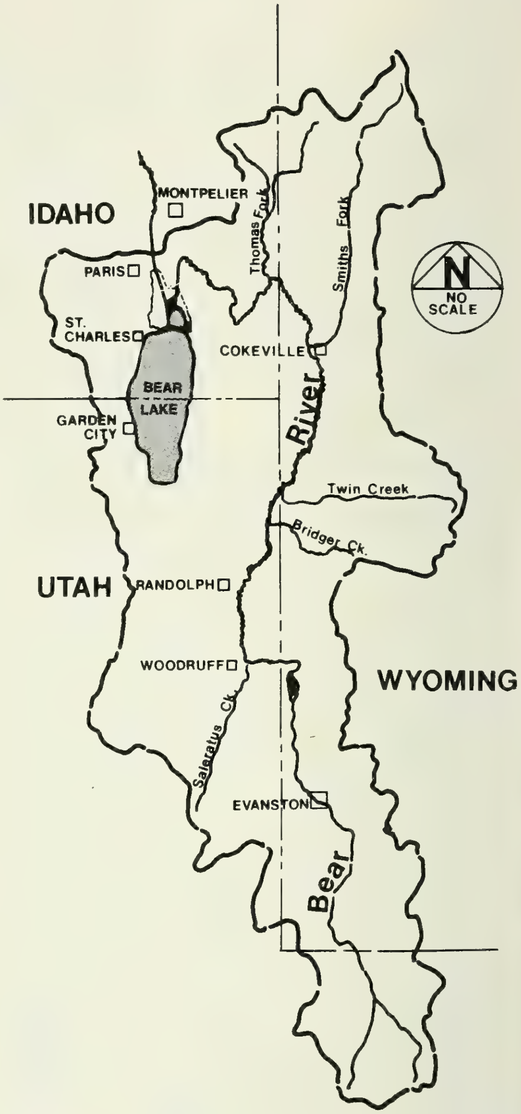

Fig. 2. A location map for Bear Lake and its watershed.

BEAR RIVER DRAINAGE.—A special portion of the Bear Lake watershed is located above the Dingle Marsh system. This watershed has only been impacting Bear Lake since 1912, when the Stewart Dam and the associated canal system was constructed. The water from the upper Bear River basin is diverted into Bear Lake during spring runoff (March–June). The annual flows at Stewart Dam for 1975 to 1984 can be seen in Figure 3. The dominant portion of the flows occurs between

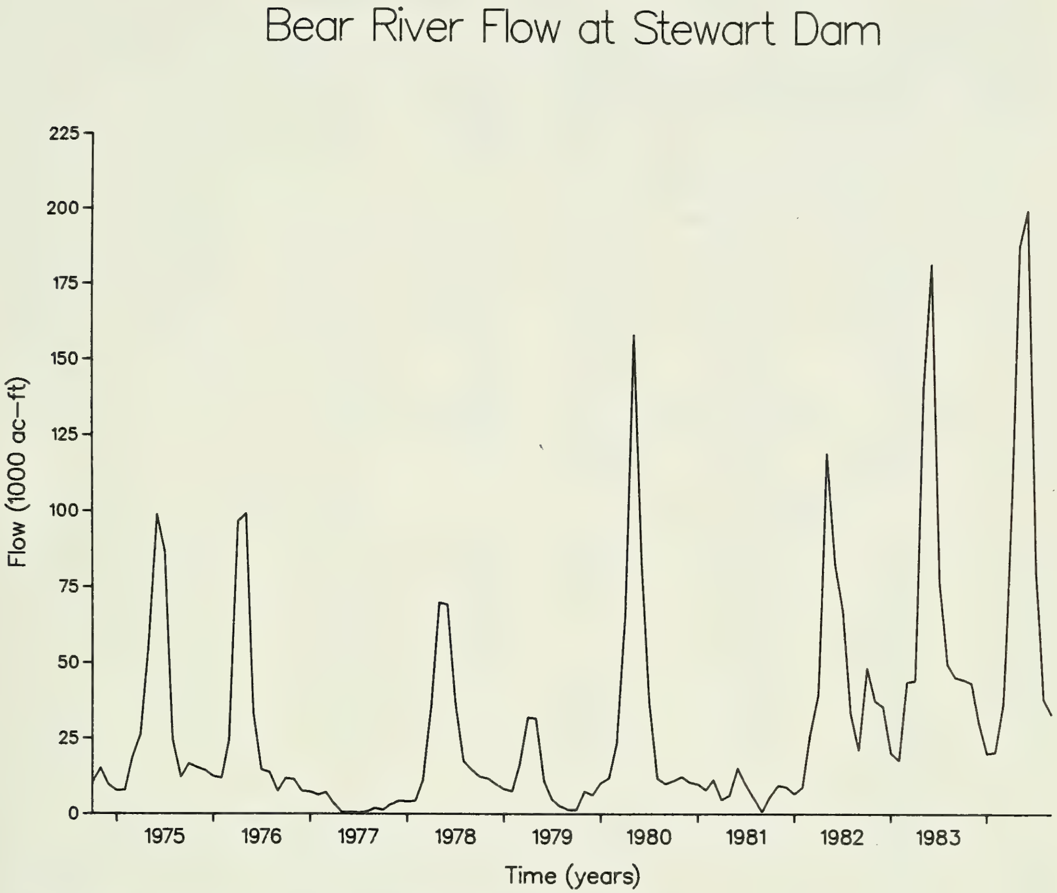

Fig. 3. The flow in the Bear River at Stewart Dam between 1975 and 1984.

March and June. In the last 10 years, the lowest volume entering the marsh was during 1977 (11,400 ac-ft) and 1981 (37,240 ac-ft). The highest volumes occurred in 1983 (411,330 ac-ft) and 1984 (492,400 ac-ft). Because of the water control structures present around the marsh, not all the water entering the system exits into Bear Lake during the spring period. For example, although 492,400 ac-ft entered Stewart Dam in 1984, 240,900 ac-ft was diverted through the outlet canal back into the Bear River, whereas the remaining 244,100 ac-ft was released through Lifton Station into Bear Lake (Table 1). The comparison of Lifton inflows to all other water sources into Bear Lake can be seen in Table 2 for the period 1975 to 1984.

Between 1975 and 1984 more than 66 sets of water quality data have been collected at the three key water control structures in Dingle Marsh (March to September). These data are also summarized in Table 1. The most complete data set are represented by total phosphorus and total inorganic nitrogen. The total phosphorus data at Lifton represents the mass loading by the Bear River into Bear Lake for 1975 and 1978 to 1984. The difference in the range of loading is significant, with 1981 being only 1,300 kg TP but 1983 being 25,838 kg TP. Ortho-phosphate was from 6.8% to 19.8% of the total phosphorus loading. In all cases, the marsh tended to remove phosphorus from the Bear River prior to its entrance into the lake. This was markedly different when compared to nitrogen and organic carbon (i.e., 1981, 1982, and 1984), when the marsh was in balance or actually increased the mass of these materials to the Bear River as it moved through the system.

BEAR LAKE WATERSHEDS AND PRECIPITATION.—Land in the Bear Lake watersheds has

TABLE 1. The mass movements of water and nutrients through key control structures around the Dingle Marsh system. The material moving through Lifton Station is the mass actually entering Bear Lake. (TP = total phosphorous; TOC = total organic carbon; TN = total nitrogen; TSS = total suspended solids; PO_4-P = orthophosphate; TIN = total inorganic nitrogen).

	Flow (AC-ftx1000) (March–June)		
Year	STD	LFT	Outlet
1975	119.61	179.34	20.27
1976	253.96	221.08	52.45
1977	11.43	9.77	111.11
1978	185.26	183.61	1.65
1979	90.36	86.44	22.28
1980	329.73	279.58	52.13
1981	37.24	34.03	28.79
1982	267.68	264.84	2.83
1983	411.33	251.50	198.97
1984	492.40	244.10	240.90

	Kg TP (March–June)		
Year	STD	LFT	Outlet
1975	11,367	9,982	10
1978	17,366	13,343	0
1979	20,669	8,551	1
1980	56,310	27,679	10
1981	6,068	1,300	3,480
1982	59,151	18,460	254
1983	75,951	25,838	26,403
1984	115,450	23,680	51,990

	Kg TOCx1000 (March–June)		
Year	STD	LFT	Outlet
1975	—	—	—
1978	—	—	—
1979	—	—	—
1980	—	—	—
1981	328	290	432
1982	3,310	7,808	32
1983	—	—	—
1984	—	—	—

	Kg TN (March–June)		
Year	STD	LFT	Outlet
1975	—	289, 042	—
1978	—	—	—
1979	—	—	—
1980	—	—	—
1981	20,693	16,579	29,284
1982	231,175	153,438	2,219
1983	578,087	137,337	138,669
1984	834,370	183,645	234,241

	Kg TSSx1000 (March–June)		
Year	STD	LFT	Outlet
1975	—	—	—
1978	—	—	—
1979	—	—	—
1980	—	—	—
1981	2,289	456	1,396
1982	63,403	13,388	193
1983	38,535	18,850	12,586
1984	73,991	22,655	41,645

Table 1 continued.

	Kg PO_4-P (March–June)		
Year	STD	LFT	Outlet
1975	—	1,602	—
1978	—	—	—
1979	2,703	582	.08
1980	13,442	5,494	0
1981	249	195	376
1982	4,263	1,244	20
1983	16,188	3,777	2,883
1984	5,435	1,155	3,151

	Kg TIN (March–June)		
Year	STD	LFT	Outlet
1975	—	27,721	—
1978	54,951	33,877	0.40
1979	15,323	13,965	1.00
1980	83,485	30,347	0
1981	5,193	3,173	4,042
1982	61,847	30,257	471
1983	24,791	12,607	6,968
1984	68,475	29,286	36,536

traditionally been used almost exclusively for rural-agricultural purposes. The high mountain lands are used primarily for grazing, watershed protection, and some recreation, whereas the land uses in the foothills surrounding the lake are grazing, dry farming, and recreational home sites. The valley floor adjacent to the lake is used for irrigated croplands, pasture for native grasses, and the major sites for summer homes and subdivisions, which are being developed at a rapid rate. The tributary discharges from the watershed for the years 1975 to 1984 can be seen in Table 2 and Figure 4. As with the Bear River, 1977 and 1981 were dry years and 1983 and 1984 were wetter than average. The associated total phosphorus budgets for these watersheds can be seen in Table 3. As can be seen from these data, 13% of the total phosphorus input into Bear Lake is by wet fall from atmospheric precipitation, whereas 20% is from the endemic watershed. The vast majority (67%) is from the Bear River at Lifton. The areal phosphorus loading (g P/m^2 Bear Lake surface/year) ranges from 0.045 g P/m^2/year to 0.136 g P/m^2/year for the five years studied.

TABLE 2. The hydrologic inputs to Bear Lake between 1975 and 1984.

	Flows (ac-ft x 1000)						
Year	Bear River (Lifton) %		Bear Lake watersheds (%)		Precipitation (%)		Total
1975	179.34	(48)	140.6	(37)	55.6	(15)	375.5
1976	221.1	(53)	119.3	(29)	74.6	(18)	415.0
1977	9.8	(8)	49.2	(41)	61.3	(51)	120.3
1978	183.6	(47)	127.6	(33)	76.5	(20)	387.7
1979	86.4	(39)	98.8	(44)	37.3	(17)	222.5
1980	279.6	(51)	174.1	(32)	96.2	(17)	549.9
1981	34.0	(23)	60.5	(41)	52.8	(36)	147.3
1982	264.8	(48)	169.0	(30)	120.3	(22)	554.1
1983	251.5	(45)	203.1	(36)	106.3	(19)	560.9
1984	244.1	(42)	264.1	(45)	73.9	(13)	582.1

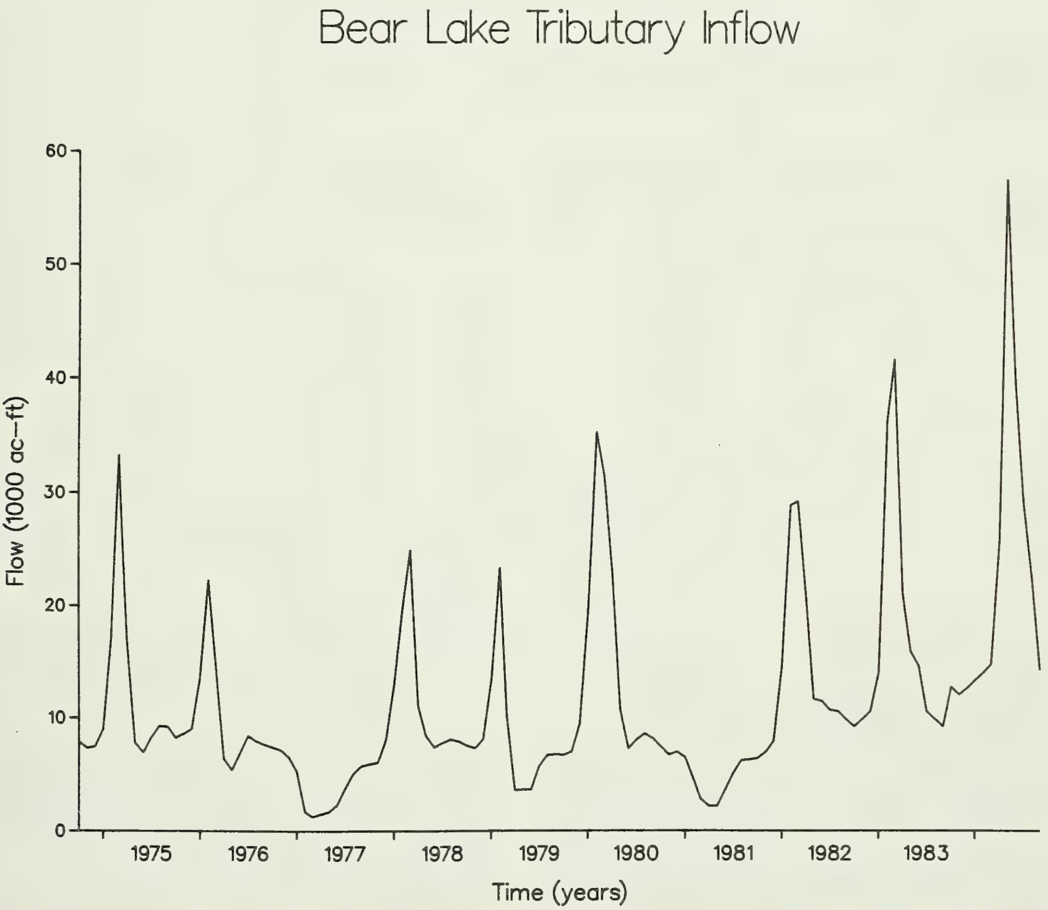

Fig. 4. The flows from the endemic Bear Lake watershed between 1975 and 1984.

BEAR LAKE LIMNOLOGY.—The first reported limnological investigation of Bear Lake was conducted in 1912 by Kemmerer et al. (1923). Since then numerous studies have been made of Bear Lake. An attempt will be made here to summarize the results of limnological investigations on the key physical, chemical, and biological characteristics of the Bear Lake ecosystem.

Bear Lake is oval shaped, about 34 km long and 14 km wide. It has an 81 km shoreline and a surface area of 284 km^2 (Fig. 1). Bear Lake

TABLE 3. The total phosphorus budgets for the major tributaries to Bear Lake for the years 1975 and 1981 to 1984.

	Years (Kg P/Year)					
Streams	1975[1]	1981[2]	1982[2]	1983[3]	1984[3]	Average percent of total
Lifton (Bear River)	9,982	8,340	18,910	28,362	24,410	67
Swan Creek	495	710	1,860	1,976	2,913	6
Big Creek	1,405	840	1,250	1,716	1,481	6
Fish Haven	125	30	570	—	—	
Little Creek	190	310	600	—	—	
North Eden	920	100	120	—	—	
Falula Spring	780	190	190	—	—	8
South Eden	—	29	40	—	—	
Irrigation return and other streams	640	88	81	2,653	2,320	
Precipitation	1,901	1,860	2,680	3,798	2,551	13
Septic tank leakage	95	260	260	260	260	<1
Total	16,533	12,757	26,561	38,765	33,935	100
Loading (g P/m^2/yr)	.058	.045	.094	.136	.121	

[1] EPA 1975
[2] Lamarra et al. 1984
[3] This study

TABLE 4. The physical and chemical characteristics of Bear Lake, Utah. Chemical characteristics are from Lamarra et al. (1984).

Physical-morphometric characteristics	
Surface area	282 km^2
Mean depth	27 m
Maximum depth	63.4 m
Volume	7.89 × 10^9 m^3
Mean hydraulic retention time	92 years
Chemical characteristics	
Alkalinity	265 mg as CaCO$_3$/l
Ca++	25 mg Ca++/l
MG++	75 mg Mg++/l
K+	3.1 mg/l
Na+	39.1 mg/l
Cl−	54.2 mg/l
SO$_4$	19.7 mg/l
Suspended solids	5.0 mg/l
Total dissolved solids	457 mg/l
Volatile suspended solids	1.5 mg/l
Total solids	475 mg/l

TABLE 5. The mean summer areal oxygen deficits (mg O$_2$/cm^2/day) Chl *a* (µg/l) concentrations in Bear Lake from 1975 to 1984.

Year	Oxygen deficits (mg O$_2$/cm^2/day)	Chlorophyll *a* (± S. E.) (µg/l)
1975	.026	—
1976	.049	0.41 ± .05
1977	.012	0.30 ± .05
1978	.049	0.66 ± .13
1979	.037	0.62 ± .06
1980	.057	0.78 ± .11
1981	.031	0.39 ± .03
1982	.043	0.59 ± .05
1983	—	0.90 ± .09
1984	.054	0.71 ± .10
Oligotrophic	<.025(1)	<.81(2)
Mesotrophic	.025–.055	.80–7.4
Eutrophic	>.055	>7.4

(1) Hutchinson 1957
(2) Vollenweider and Kerekes 1980

has been described as dimictic with a distinct thermocline at 15–17 m. Summer surface temperatures range bewteen 20C and 22C, and hypolimnetic temperatures are usually below 7C. The maximum temperature fluctuations of hypolimnetic water below 50 m have been found to be 2C to 7C. Part of the north and northwest shores of the lake are covered with emergent plants. The remaining shoreline is composed of sand and rock. However, the rocky zone is not extensive, extending only 4 m into the lake. Hypolimnetic sediments are made of marl.

The macrochemical constituents found in Bear Lake are rather unique in their relative abundance (Table 4). Each investigation on Bear Lake has shown that $Mg^{++}>CA^{++}>Na^{+}>K^{+}$ and $HCO_3^{-}>CL^{-}>SO_4^{=}>CO_3^{=}$. Conductivities range between 720 and 680 umhos/cm at 25C and pH between 8.3 and 9.0. The surface oxygen concentrations during the summer in Bear Lake are near saturation, based on temperature and pressure. However, hypolimnetic concentrations were found to be less than 50% of saturation. The mean summer areal oxygen deficits (rate of oxygen loss in the hypolimnion) between 1975 and 1984 can be seen in Table 5.

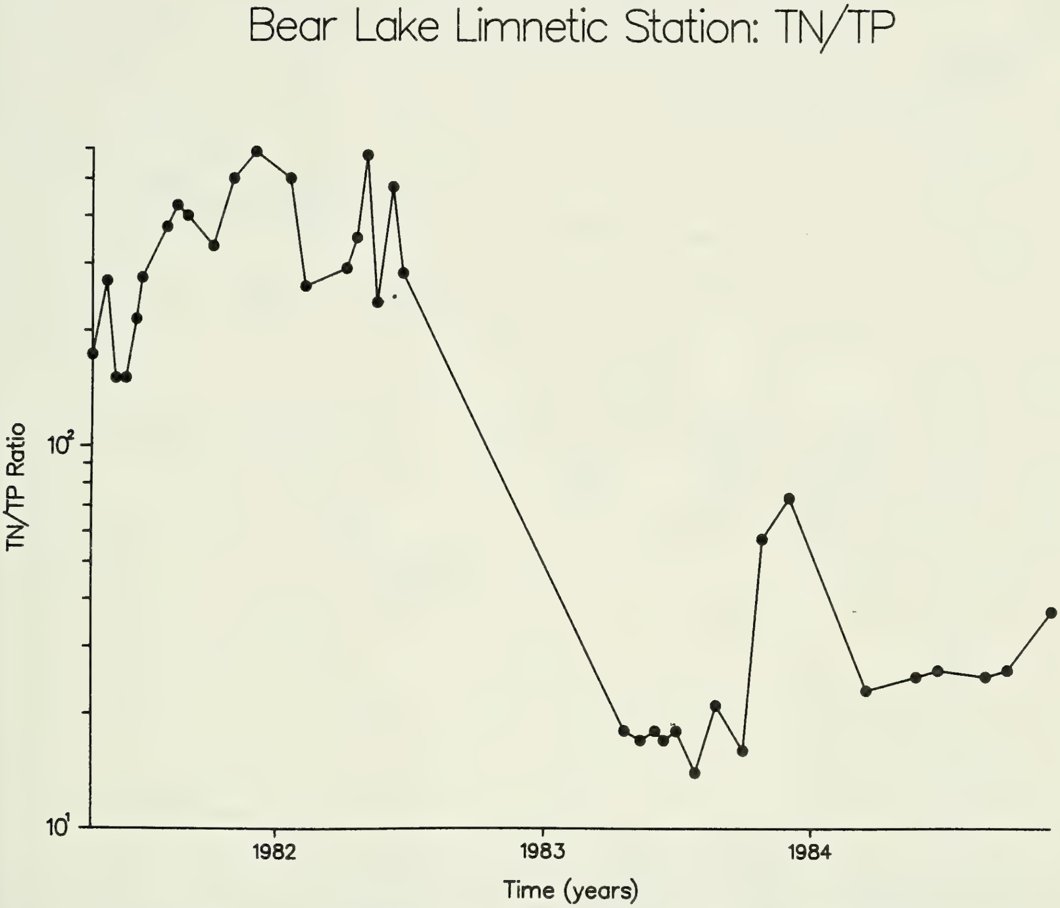

Fig. 5. The total nitrogen to total phosphorus ratio for the surface and 10 m station in Bear Lake between 1981 and 1984. Phosphorus was found to be limiting TN:TP ratio >17, 88% of the time.

An initial analysis of the limnetic nutrient data has indicated that phosphorus appears to be the dominant limiting element in the Bear Lake system (Fig. 5) and therefore the nutrient of most concern. Furthermore, the mean summer total phosphorus concentrations in the epilimnion of Bear Lake have been steadily increasing over the last nine years (Fig. 6).

Because of the uniform shoreline in Bear Lake, rooted plants in the littoral zone of the lake are scarce, therefore relegating the dominant primary production in the lake to the limnetic phytoplankton. The seasonal distribution of the surface (epilimnetic) and subsurface (metalimnetic) phytoplankton biomass can be seen in Figure 7. These data indicate that during the summer months the highest density of phytoplankton occurs between 20 and 30 m below the surface (metalimnetic). In addition, the average summer surface chlorophyll *a* concentrations for 1976 through 1984 are provided in Table 5. Although these data are not representative of the highest algal densities, they do provide a historical perspective of water quality changes within the surface waters of Bear Lake.

DISCUSSION

The limnological conditions present in Bear Lake over the last decade provides some interesting insights into the temporal dynamics of this lake ecosystem. The algal biomass in the lake (expressed as a spring-summer average for chlorophyll *a*) has increased in concentration since 1976, reaching a maximum in 1983 and declining slightly the following year

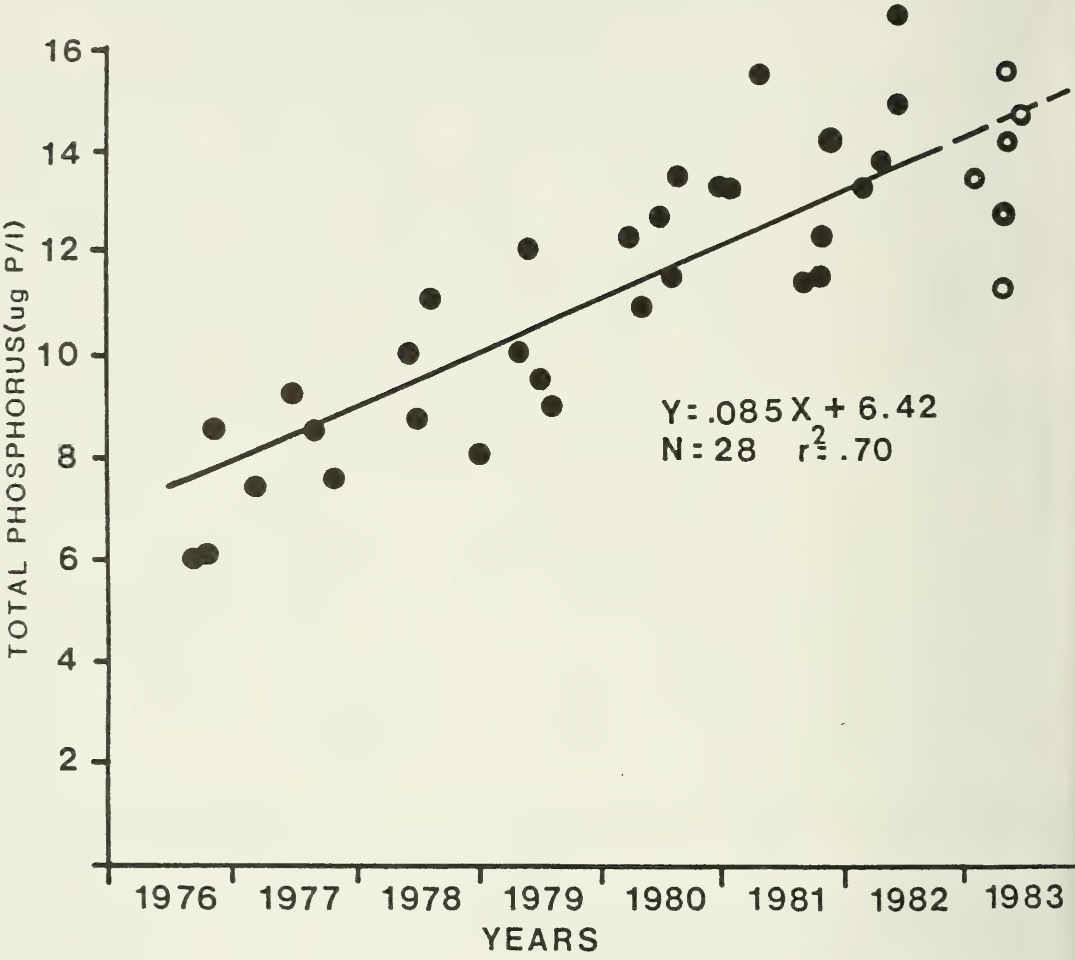

Fig. 6. The mean summer months (April–September) total phosphorus concentrations from the epilimnion of Bear Lake. Sources of the data are from Lamarra et al. 1984.

(Table 5). In a similar manner, areal oxygen deficits (Table 4) and phosphorus loading (Table 2) have demonstrated a year-to-year fluctuation.

The concept of a trophic classification for lake ecosystems has long been recognized. Early studies investigated the quality of plankton and have been summarized by Rawson (1956). More recently, trophic state has been defined by nutrient loading (Vollenweider 1976), complex ecosystem models (Simon and Lam 1980, Ditoro and Matystik 1980), and the interrelationships of a variety of parameters (Porcella 1980). A coarse resolution technique used by Carlson (1977) resulted in using single but interrelated parameters. Total phosphorus, chlorophyll *a*, and Secchi disk transparency have been shown to provide an excellent basis for a trophic state index (TSI). However, because of the presence of $CaCO_3$ precipitates in Bear Lake and its effect upon phosphorus availability, Chl *a* was determined to be the most representative parameter for a TSI calculation. A comparison has therefore been made in Table 6 between the Chl *a* TSI value, areal phosphorus loadings (g P/m^2/year), and areal hypolimnetic oxygen deficits (mg O_2/cm^2/day). In each case the static (TSI), dynamic (areal oxygen deficits), and predictive (areal phosphorus loadings) trophic state classifications indicate that Bear Lake is upper olig-

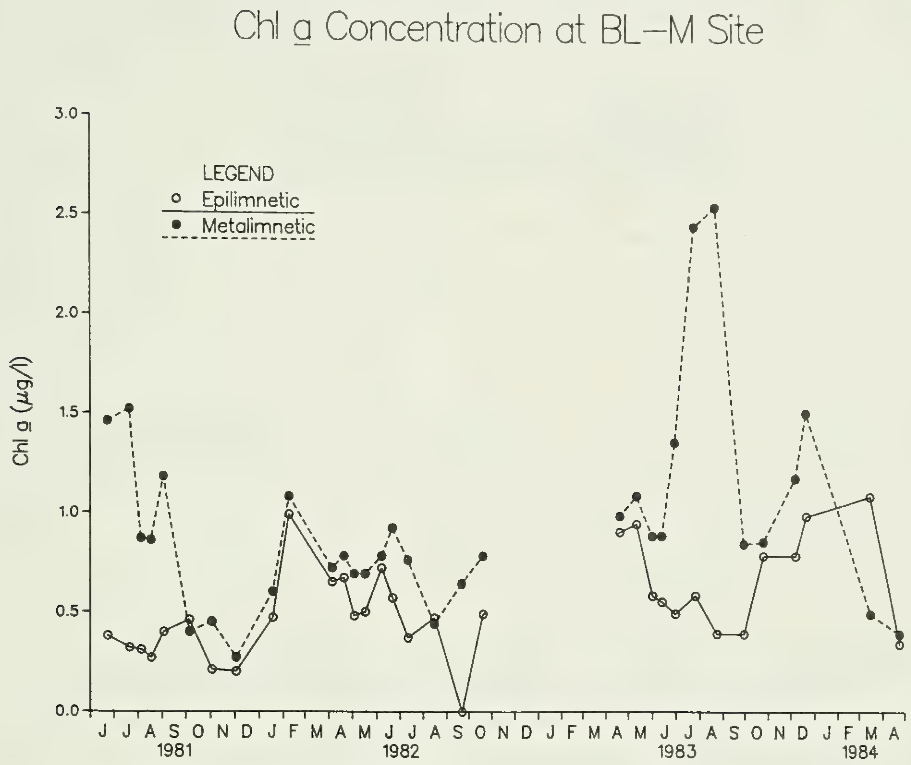

Fig. 7. The temporal distribution of chlorophyll *a* in the epilimnion (surface and 10 m) and metalimnion (20 and 30 m) in Bear Lake, Utah-Idaho.

TABLE 6. The estimated TSI values (Carlson 1977) for chlorophyll *a*, the areal oxygen deficits (mg O_2/cm^2/day), and the total phosphorus areal loadings (g P/m^2/yr) for Bear Lake between 1975 and 1984.

I. TSI parameter (chlorophyll *a* µg/l)	N = 140	TSI values
Average (1975–1984)	0.60	29
Range	.19–3.0	14–45
Oligotrophic(1)	<.80	<30
Mesotrophic	.80–7.4	30–60
Eutrophic	>7.4	>60
II. Areal oxygen deficits (mgO_2/cm^2/day)		N = 9
Average (1975–1984)		.040
Range		.012–.057
Oligotrophic(2)		<.025
Mesotrophic		.025–.055
Eutrophic		>.055
III. Areal phosphorus loading (g P/m^2/yr)		N = 5
Average 1975 (1981–1984)		.090
Range		.058–.136
Oligotrophic(3)		<.07
Mesotrophic		.07–.15
Eutrophic		>.15

(1)Carlson 1977
(2)Hutchinson 1957
(3)Vollenweider 1976

otrophic to strongly mesotrophic. Because Bear Lake has been previously classified as oligotrophic (Kemmerer et al. 1923), the driving factors for the observed trophic changes need to be elucidated. The limnological trends presently observed in the lake may be the result of increased human activity within the basin, increases in the hydrologic inputs, or a combination of these factors. Comprehensive sets of water quality data for the Bear River, Bear Lake watersheds, and Bear Lake do not exist prior to 1975. As an alternative to a historical data base, inferences to previous water quality conditions in Bear Lake can be made from the extensive hydrological data available. Based upon the data presented here, a series of regression equations were produced that indicated the watershed loadings of phosphorus and inlake water quality parameters (summer chl *a* and oxygen deficits) were significantly related to mass flows from the watersheds (Table 7). Based upon these statistical relationships and the historical flow data, hydrologic and nutrient budgets were developed for the recent history

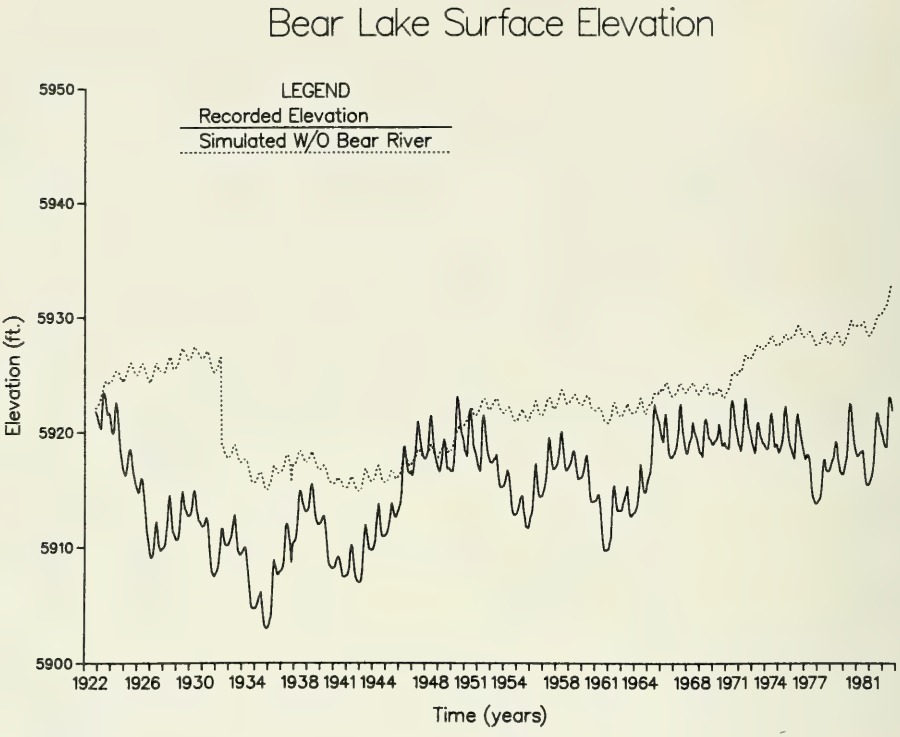

Fig. 8. The simulated elevations in Bear Lake without the Bear River and the natural elevations with the operation of the Bear River storage system between 1924 and 1984.

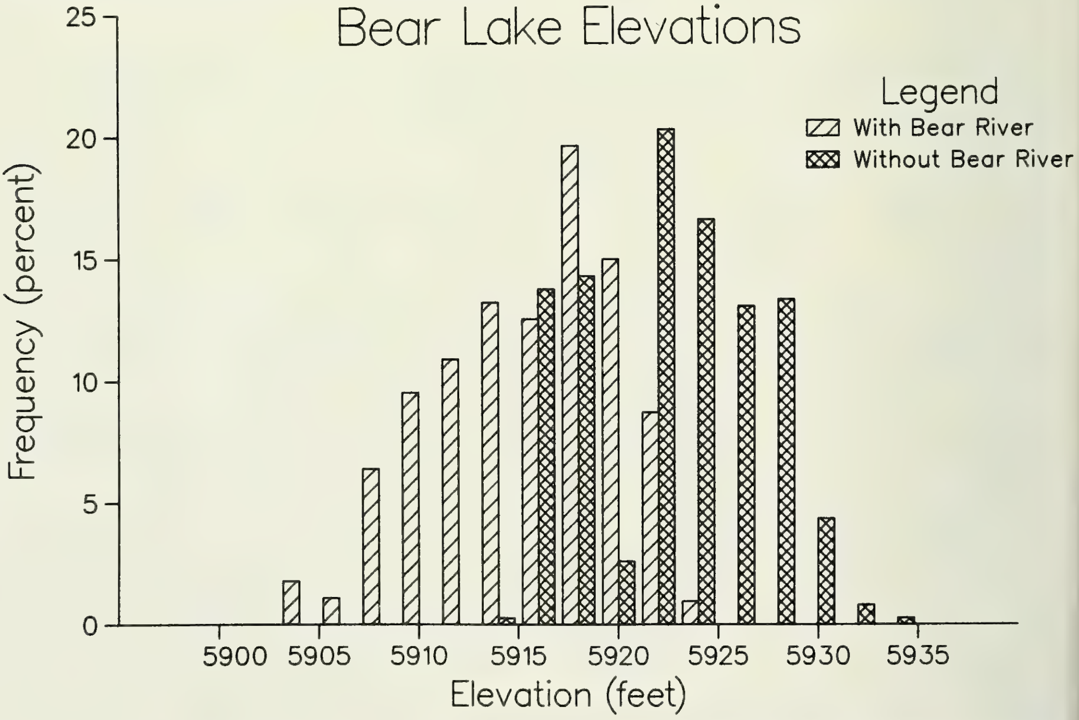

Fig. 9. A frequency distribution of monthly Bear Lake elevations (1924 to 1984), with a simulated watershed excluding the Bear River and actual elevations with the Bear River.

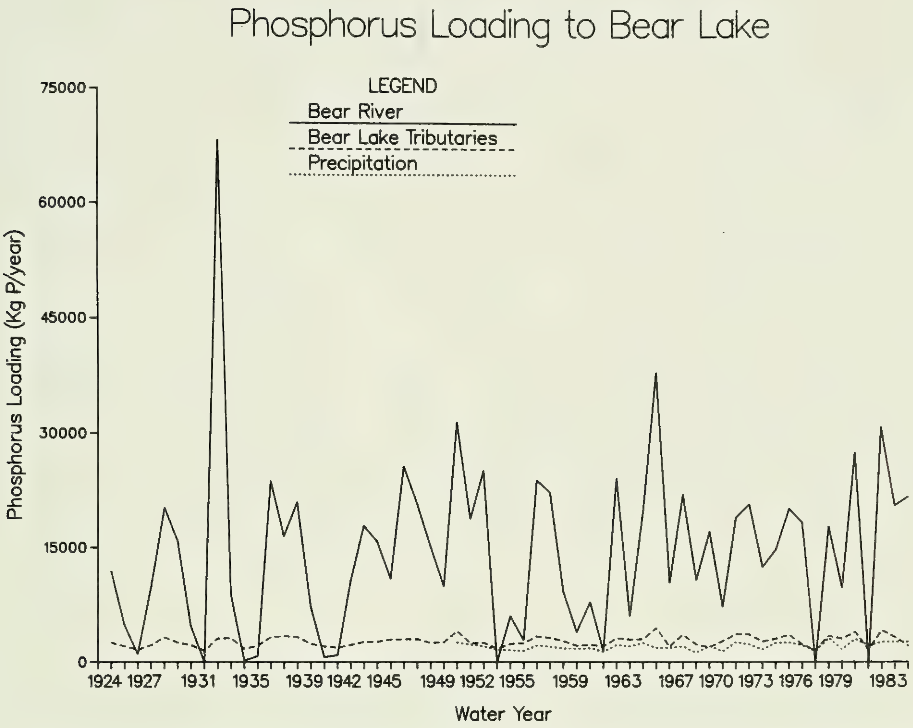

Fig. 10. The estimated mass (kg P/year) of phosphorus entering the Bear Lake system between 1924 and 1984.

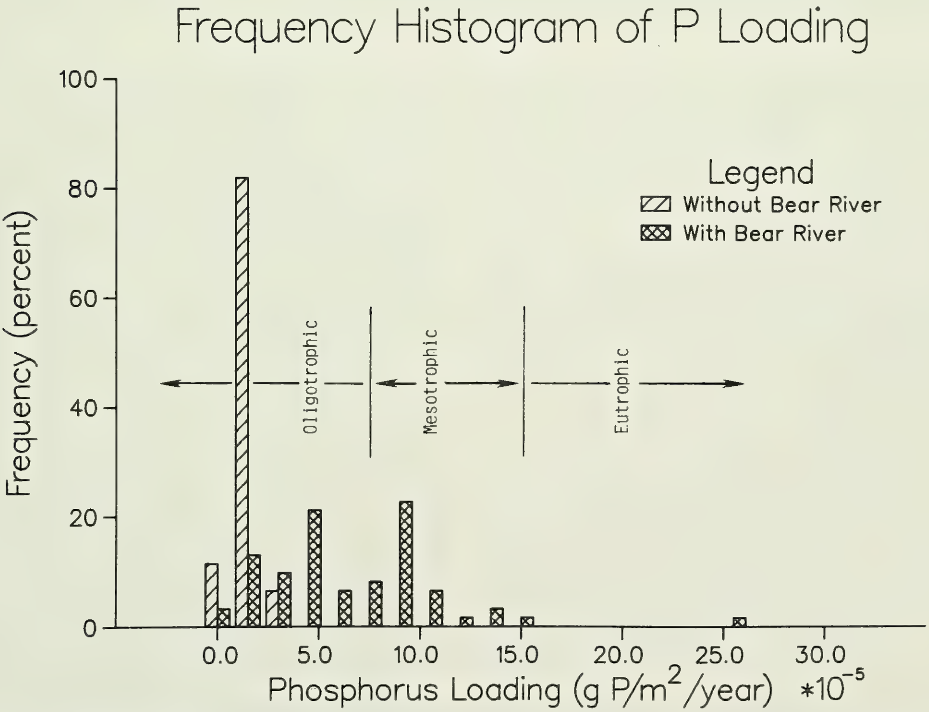

Fig. 11. The frequency distribution of areal total phosphorus loading (g P/m^2/yr) for Bear Lake with and without the Bear River for the period 1924–1984.

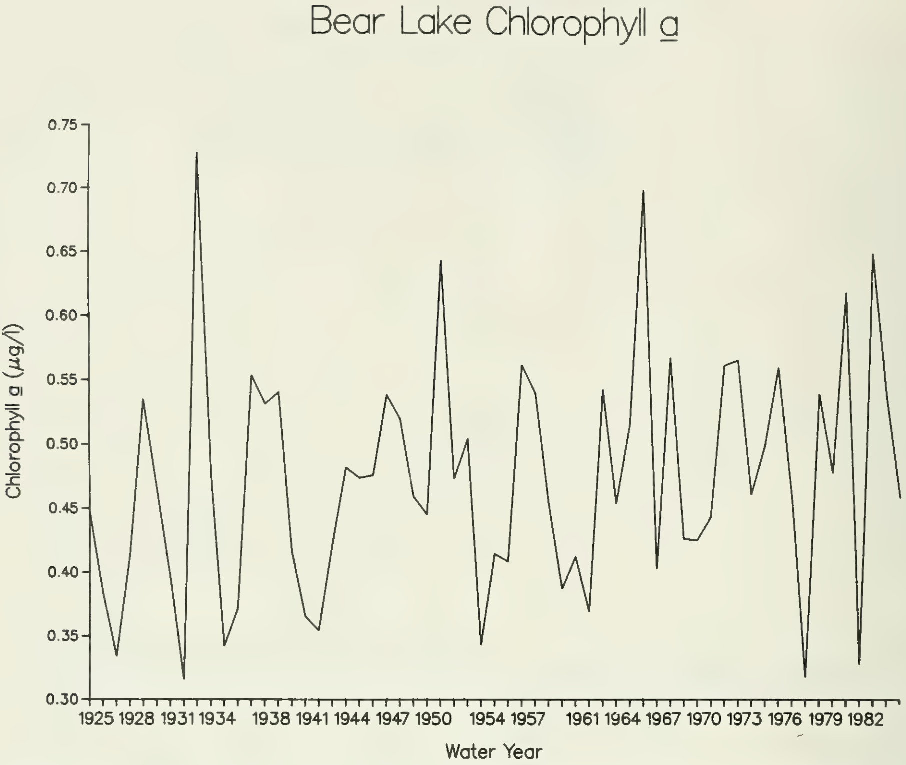
Bear Lake Chlorophyll a

Fig. 12. The historical distribution of mean summer chlorophyll *a* concentrations as simulated from the empirical relationships developed from the years 1975 through 1984.

(1923–present) in Bear Lake with and without Bear River inflows. The major assumption made in this analysis was that the historical water quality in the Bear River had not significantly changed and is similar to the period 1975–1984.

The hydrologic budget for Bear Lake was developed using all sources and losses on a mass balance basis. Input data for equation (1) was obtained from Utah Power and Light Company.

$$\triangle S = (I - O) - S \qquad (1)$$

where: $\triangle S$ = Annual change in Bear Lake storage (ac-ft/year)
I = Rainbow canal inflow (ac-ft/year)
O = Outlet canal flow (ac-ft/year)
S = Actual Bear Lake storage from elevation capacity curves (ac-ft/year)

The results of this analysis, with and without the Bear River inflows can be seen in Figure 8. The data indicate that the simulated elevations in Bear Lake without the river were higher (except for the years 1944–1950) than the lake elevations with the river inflow-outflow manipulations. The estimated elevations of the lake indicated that the threshold of 5,927.0 ft between Bear Lake and the marsh complex would have been exceeded about 24% of the time during the last 60 years (Fig. 9), providing a direct connection between the shallow marsh in the northern valley and the lake to the south. In addition, the simulation indicates that during the 1970s the lake would have had a steady increase in elevation above 5,924 ft to a high elevation of 5,935 ft in 1984. This increase in lake elevation would inundate the confluence of the Bear River and the Bear Lake valley, thus naturally adding a 7,000 km^2 watershed to the Bear Lake drainage.

During the same time period simulated in the hydrologic budgets, the annual phosphorus loading (kg/year) by source was estimated (Fig. 10). It appears that about 60% of the historical loading to the lake can be attributed

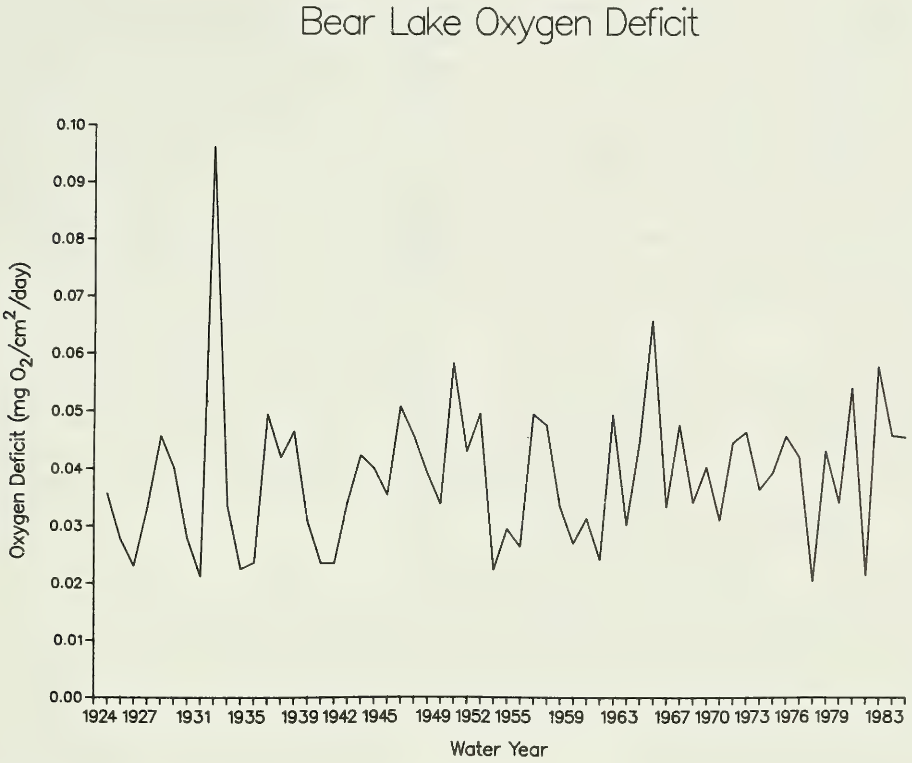

Fig. 13. The historical distribution of mean summer areal oxygen deficits (mg O_2/cm^2/day) as simulated from the empirical relationships developed from the years 1975 through 1984.

to the Bear River, and in only 10 years of the last 60 has the endemic watershed produced more phosphorus loading than the Bear River. A frequency analysis of areal phosphorus loadings indicates that with the presence of the Bear River, 58% of the last 60 years the loading could be considered oligotrophic, while 42% could be considered mesotrophic or eutrophic. In contrast, without the Bear River inflows 100% of the annual loadings would be oligotrophic (Fig. 11).

In a similar manner, the simulation of the historical chlorophyll *a* and areal oxygen deficits (Fig. 12, 13) with the presence of the Bear River demonstrates the importance of this water source in modifying the Bear Lake environment. Frequency histograms for both parameters (Fig. 14, 15) demonstrate patterns similar to those expressed by areal phosphorus loadings, indications that the Bear River may have shifted the trophic state of Bear Lake from oligotrophic to mesotrophic.

The Bear Lake ecosystem is a unique environment. Because of its isolation for more than 8,000 years, the biological community has evolved into a simple, coexisting trophic structure, with four endemic species of fish. The uniqueness of the Bear Lake community lies in the adaptations of the organisms to one another and the importance of the endemic fish to the overall trophic structure. For example, the cisco is a dominant food item of the large predators and is, itself a planktivore, feeding exclusively on zooplankton within the metalimnion during summer stratification. In turn, the zooplankton community has few large cladocerans, with its structure dominated by a large *Epischura* sp. This organism has adapted a swift predatory escape mechanism. Because the effect of water quality changes upon these species is unknown, defining the driving factors and their degree of impact upon changes in water quality may provide management alternatives for this ecosystem.

The results of this preliminary investigation have inferred the historical impacts of the Bear River inflows upon the limnological con-

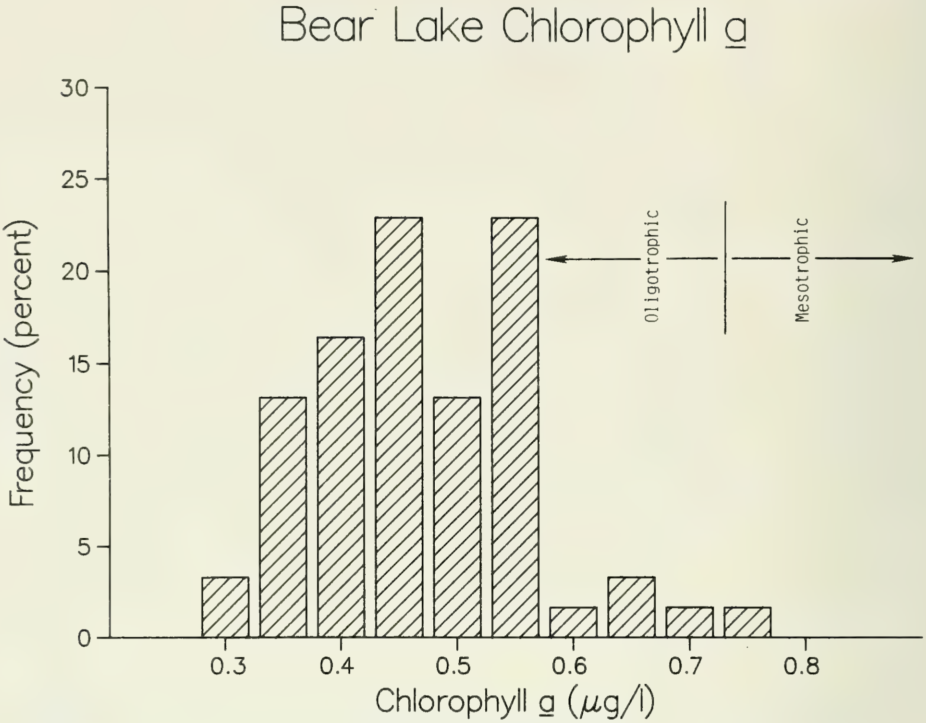

Fig. 14. A frequency histogram of the simulated mean summer chl *a* concentrations (μg/l) for the years 1924 through 1984.

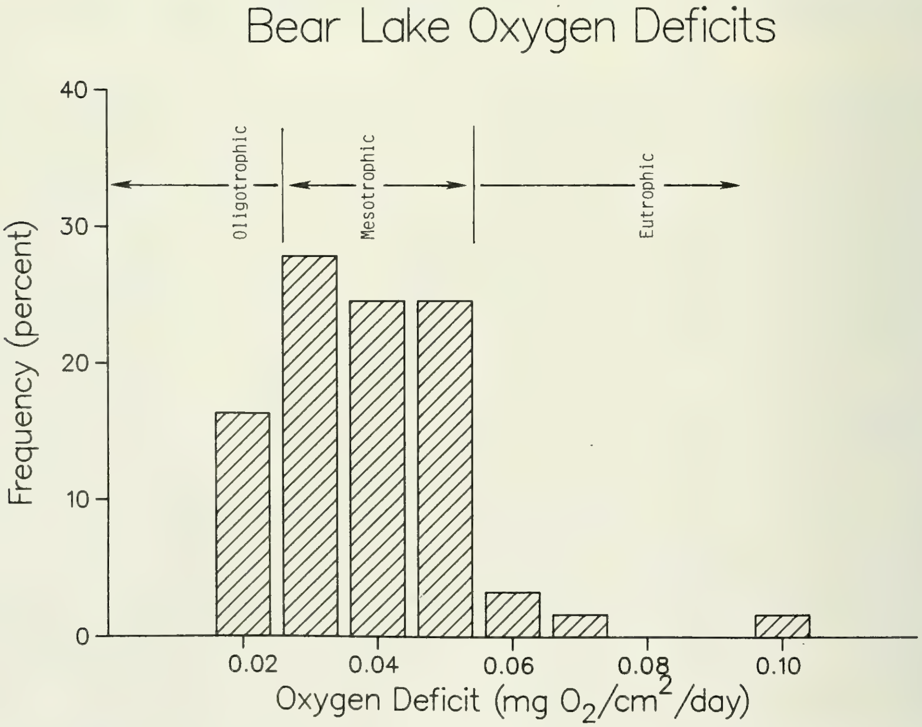

Fig. 15. A frequency histogram of the simulated mean summer areal deficits (mg $O_2/cm^2/day$) for the years 1924 through 1984.

ditions in Bear Lake, based upon 9 years of empirical limnological data and 60 years of historical flows. This impact has been extensive. In addition, the future human developments of the Bear Lake basin will only increase the nutrient export from the watershed to the lake environment. Mitigation measures that directly address sources of nitrogen and phosphorus within the watersheds must be developed. Increased eutrophication may result in the loss of several if not all of the endemic species. In a similar manner, the investigation of alternative hydrologic storage of the Bear River as it relates to Bear Lake seems advisable. The development of 100,000 ac-ft of storage above Bear Lake may reduce previously described oxygen deficits and cut the phosphorus loading by 7,000 kg/year.

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UNDERSTORY SEED RAIN IN HARVESTED PINYON-JUNIPER WOODLANDS

Richard L. Everett[1]

Abstract.—Seed rain was collected on six paired tree harvest and undisturbed plots in singleleaf pinyon (*Pinus monophylla*)–Utah juniper (*Juniperus osteosperma*) stands. Approximately 14,600 seeds were collected during four years. Seed rain in undisturbed plots was similar to levels in mixed forest communities. Seed rain on harvest plots was similar to disturbed sites and grasslands. Seed rain levels reflect the current successional stage rather than the climax community type for the site. Seed rain increased in numbers and seed production per unit of plant cover following tree removal and especially on transition soil microsites. Only three to four of the plant species present on a site contributed greater than 10% of the total seed rain. Seed rain composition was similar on harvest and undisturbed plots (Jaccard Similarity Index Values = 47% to 67%) and explains in part the rapid reestablishment of predisturbance understory communities.

Understory response to tree harvesting is dependent upon remnant plants (Dyrness 1973, Lyon and Stickney 1976), soil seed reserves (Oosting and Humphreys 1940), and seed rain (Rice et al. 1960). Seed rain, the dissemination of seed and its dispersal, varies among species and plant communities (Harper 1977). Plant strategies in part control the amount of resources a plant commits to seed production and the impact the species has on community seed rain (Grime 1977, Everett and Sharrow 1983).

Seed rain declines exponentially with distance from the parent plant (Werner 1975, Harper 1977). But seeds are often transported across the soil surface until they lodge against protuberances or depressions (Knipe and Springfield 1972). Nelson and Chew (1977) found greatest concentrations of soil seed reserves in the Mojave Desert, adjacent to shrub canopies, and hypothesized that shrub litter areas acted as seed rain catchments. In pinyon-juniper woodlands soil seed reserves were greatest at the edge of the tree crown (Koniak and Everett 1982).

Seed rain composition changes abruptly from one year to the next in forests. This in part is due to the abrupt appearance and disappearance of species during forest succession (Oosting and Humphreys 1940) and variable annual precipitation (Duba and Norton 1976).

This paper reports on a four-year study of seed rain following tree harvesting in singleleaf pinyon (*Pinus monophylla* Torr. & Frem.)–Utah juniper (*Juniperus osteosperma* [Torr.] Little) woodlands. Seed rain was observed on three grass and annual forb understory sites for four years and three shrub and annual forb understory sites for two years. The null hypotheses to be tested were: (1) there are no differences in seed rain numbers or composition between harvest and undisturbed plots or soil microsites, (2) seed rain is evenly distributed among plant forms and reflects species composition, and (3) seed rain production per unit of cover remains constant following tree harvest. Increased seed rain following tree harvest would promote rapid establishment of understory and if related to floristic composition would increase predictability of plant response.

Field Methods and Data Analysis

Previous study sites in stands of singleleaf pinyon–Utah juniper on the Sweetwater and Shoshone mountain ranges were selected for study. The Sweetwater site lies above alluvial fans that are dominated by mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana*) and below a ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) community. The site has an average annual precipitation of 266 mm. Fully stocked stands have a remnant mountain big sagebrush–annual forb understory. The three plots used for the study had a similar east exposure (N 70° E) but varied in elevation from 2,040 to 2,280 m.

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The Shoshone site lies between communities of higher elevation mountain big sagebrush and lower elevation Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis*). The site has an annual precipitation of 330 mm. The three study plots are on north- (N 20° E), west- (S 84° W), and south-facing (S 16° E) aspects at approximately the same elevation (2,300 m). Understory is sparse but includes perennial grasses: Idaho fescue (*Festuca idahoensis* Elmer), Sandberg bluegrass (*Poa sandbergii* Vasey), bottlebrush squirreltail (*Sitanion hystrix* Nutt.); perennial forbs: Hood's phlox (*Phlox hoodii* Rich.), hollyleaf clover (*Trifolium gymnocarpum* Nutt.); and an array of annual forbs.

The soil surface in both woodland study areas is a mosaic of soil microsites: a dense needle duff under the tree, scattered needle cover in a transition zone at the crown edge, and bare ground in the interspace between trees. These soil microsites vary in species composition and productivity (Everett 1984).

Three 30 by 30 m square plots previously clear-cut of all trees greater than 1 m in height were used at Shoshone and Sweetwater sites. Sweetwater plots were cut in 1977 and Shoshone plots in 1979. Trees and slash were removed from the sites by hand with minimal disturbance to the plots. Areas of similar floristic and topographic appearance were selected adjacent to cut areas to serve as undisturbed controls.

Shoshone plots were sampled for seed rain in the first and second years following harvest (1980 and 1981) using 12 seed traps randomly placed on four duff, four transition, and four interspace soil microsites at each of the three harvest and control plots. The study was expanded in 1982 and 1983 to include three paired harvest and control plots at the Sweetwater site (five and six years following harvest). Sampling intensity was increased to 24 seed traps in each harvest and undisturbed plot at Sweetwater and Shoshone sites in 1982.

Seed traps were emptied of seed every 2 to 3 weeks from May to October. Traps were left in the field during the winter months and inspected the following spring. A seed voucher was made for all plant species encountered on the sites. Seeds collected in the traps were compared with voucher specimens for correct identification.

Seed traps consisted of 90 mm dia. petri dishes coated inside with an adhesive (Tanglefoot[2]), as suggested by Werner (1975). Each dish had a central hole (3 mm dia.). We placed a screen (5 mm mesh) over the traps to prevent predation by rodents and inserted a nail through the screen and dish to hold the trap on the soil surface.

Differences in seed rain among harvest and undisturbed plots and among soil microsites were compared in analysis of variance tests using Hartley's Sequential method of testing to identify significant differences between means (Snedecor and Cochran 1978).

To measure plot understory cover, five permanent transects (20 m) were established in each plot. Shrub cover was estimated by line intercept (Canfield 1941). Herbaceous species cover was estimated by the Daubenmire (1959) canopy coverage method using sampling frames (50 x 50 cm) laid down at each meter mark. In addition, we centered circular sampling frames (50 cm dia.) over each seed trap and estimated plant cover of seed producing species.

Relationships between seed rain and plant cover of seed-producing species were evaluated by linear regression. Similarity between plot seed rain and floristic composition was evaluated using Jaccard Similarity Index Value (SIV) (Mueller-Dombois and Ellenberg 1974).

$$\mathrm{SIV} = \frac{\mathrm{CS} \times 100}{(\mathrm{CS} + \mathrm{SSR} + \mathrm{SFC})}$$

Where: CS = species common to seed rain and floristic composition
SSR = species in seed rain only
SFC = species in floristic composition only

Similarities in seed rain and floristic composition between harvest and undisturbed plots were also compared.

RESULTS AND DISCUSSION

We collected 14,676 seeds in seed traps from 1980 to 1983. Understory seed rain was

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[2] The use of trade, firm, or corporation names in this paper is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Agriculture of any product or service to the exclusion of others that may be suitable.

TABLE 1. Mean seed rain (seeds/dm^2) on tree harvest and undisturbed plots.

Year	Shoshone		Sweetwater	
	Harvest	Undisturbed	Harvest	Undisturbed
	(seeds/dm^2)			
1980	$20.3^{.05}$[1]	2.9	—	—
1981	$35.0^{.05}$	1.6	—	—
1982	$23.9^{.05}$	5.0	$10.4^{.05}$	1.6
1983	$98.3^{.05}$	3.9	$61.9^{.05}$	19.9

[1] Significant difference ($p = 0.05$) between harvest and undisturbed plots.

TABLE 2. Seed rain (seed/dm^2) by community types

Seed rain	Plant community	Citation
1,000	Meadow	Mortimer 1974
115–500	Alien annuals	Duba and Norton 1976
20–98	Disturbed woodland	(this study)
24–42	Mine waste–prairie	Archibold 1980a
22	Grassland	Knipe and Springfield 1972
2–20	Woodland	(this study)
3–9	Mixed forest	Archibold 1980b

TABLE 3. Mean proportion of seed rain by plant form for Shoshone and Sweetwater sites for the study period.

	Shoshone		Sweetwater	
	Harvest	Undisturbed	Harvest	Undisturbed
	(percent)			
Annual grass	0.0	0.5^b	0.0	0.0
Perennial grass	36.8^b	59.3^a	$.9^b$	3.0^b
Annual forb	63.2^a	39.5^a	99.1^a	97.0^a

Values in the same column with different superscripts are significantly different ($p = 0.05$).

estimated at 1.6 to 20 seed/dm^2 in undisturbed stands and from 10 to 98 seeds/dm^2 in harvested plots (Table 1). Seed rain was always greater on harvested than on undisturbed stands. This in part explains previous findings that soil seed reserves decline rapidly from early to late successional stages (Koniak and Everett 1983). Seeds/dm^2 equates to millions of seeds per hectare. Undisturbed pinyon-juniper woodlands had seed rain totals similar to mixed forest communities in Canada (Archibold 1980a). These levels are lower than in other community types (Table 2). Seed rain on tree harvest sites approximates seed rain levels reported for disturbed sites and grasslands.

On the Shoshone site, plant-form composition of seed rain on harvested sites was grass 37% and forbs 63%, and on the undisturbed sites grass 59% and forbs 39% (Table 3). Seed rain on Sweetwater sites was composed almost entirely of annual forb seeds (97% to 99%) on harvested and undisturbed sites. Annual forbs produce copious amounts of seed (Biswell and Graham 1956, Archibold 1980a, b), but populations of annuals change dramatically from one year to the next (Treshow and Allan 1979). Although shrub and perennial forb species were present on both sites, their seed made up less than 1% of the seed rain. Lodging of mountain sagebrush seed stalks by snow was observed and seed dissemination may not have occurred. At both Shoshone and Sweetwater sites the proportion of annuals in seed rain declined in undisturbed stands.

Only three to five species made greater than 10% contribution to total seed rain on any site. On Shoshone plots squirreltail bottlebrush and Sandberg bluegrass each contributed 10% to 50% of the total seed rain. The annual forb *Cryptantha watsonii* (A. Gray) Greene made up 16% to 25% of total seed rain on harvest plots but only 1% on undisturbed sites. *Microsteris gracilis* (Hook.) Greene contributed to the seed rain (11% to 21%) on both harvested and undisturbed plots.

Seed rain on the Sweetwater site was dominated by an array of annual species including *Collinsia parviflora* Dougl. (7% to 54%), *Cryptantha watsonii* (0% to 22%), *Gayophytum ramosissimum* Nutt. (5% to 32%), *Gilia gilioides* (Benth.) Greene (1% to 17%), *Microsteris gracilis* (1% to 23%), and *Phacelia humulis* Torr. and Gray (2% to 20%). Archibold (1980a,b) previously reported the dominance of seed rain by annual forb species on disturbed sites.

Seed rain composition does not mirror floristic composition. Shoshone and Sweetwater sites had Jaccard Similarity Index Values (SIV) of 23% to 78% between floristic composition and seed rain (Table 4). The proportion of perennial species that contributed to seed rain (58%) was significantly less ($p=0.05$) than the proportion of annual species (80%). Annuals must set seed crops frequently, whereas perennials can forego seed production and still maintain a position in the plant community. SIV values were somewhat lower on the Shoshone site because of a greater proportion of perennial species (55% to 59%) than occurred on Sweetwater sites (26% to 48%).

TABLE 4. Similarity index values between seed rain and plant composition on harvest and undisturbed plots.

	1982		1983	
	Harvest	Undisturbed	Harvest	Undisturbed
		(percent)		
Sweetwater	78	71	23	65
Shoshone	29	31	39	33

Jaccard's Similarity Index Values (Mueller-Dombois and Ellenberg 1974). Maximum SIV = 100.

TABLE 5. Seed rain per dm^2 cover of seed-producing species by soil microsite.

Duff		Transition		Interspace	
Harvest	Undisturbed	Harvest	Undisturbed	Harvest	Undisturbed
		Shoshone			
$3.5^{.05}$[1]	.57	$4.18^{.05}$	.57	$3.95^{.05}$	.97
		Sweetwater			
$5.11^{.05}$	1.43	$9.14^{.05}$	.65	1.56	.27

[1]Slope (b) from regression of species seed rain on species cover significantly different ($p = 0.05$) than 0 based on t-values.

TABLE 6. Proportion of seed rain by soil microsites on harvest and undisturbed plots.

Harvested			Undisturbed		
Duff	Transition	Interspace	Duff	Transition	Interspace
			Shoshone		
28.0^b	45.0^a	26.8^b	17.0	40.5	42.8
			Sweetwater		
25.5^b	51.5^a	23.5^b	22.0	34.0	44.0

Site values in the same row with different superscripts are significantly different ($p = 0.05$).

Cover of seed-producing species adjacent to the seed traps was significantly (regression slope greater than 0) related to seed rain on harvest plot soil microsites (Table 5). Seed rain per unit area of plant cover was greater on harvested than on undisturbed plots for all soil microsites. Cover on harvested plots produced 1.56 to 9.14 seeds per dm^2 of cover, whereas undisturbed plots produced 0.27 to 1.47 seeds per dm^2 of cover. In 1983 understory cover on harvest plots (mean = 24.4%) was significantly greater ($p=0.05$) than that on undisturbed plots (mean=7.7%) (five of six plots). Both the quantity of understory and its ability to produce seed increased following tree removal.

Seed rain was greater on the transition soil microsite than duff or interspace in the Shoshone and Sweetwater harvest plots (Table 6). Differences in seed production among microsites were less apparent in undisturbed stands. Tree competition in undisturbed stands may reduce differences in potential understory seed production among microsites. Differences in seed rain among microsites may reflect and maintain previously described differences in understory species distribution (Everett 1984).

Similarity values for seed rain between harvested and undisturbed plots ranged from 47% to 67% for both sites in 1982 and 1983. Similarity values for floristic composition ranged from 43% to 68% during this time. Tree harvest alters understory composition, but the similarity in seed rain is likely to be a contributing factor to the rapid reestablishment of predisturbance woodland communities following tree harvest and burning (Everett 1984, Everett and Ward 1984).

CONCLUSIONS

Seed rain increased following tree harvesting. Seed rain of 10 million to 98 million seeds per hectare fell to the soil surface in harvested pinyon-juniper woodlands. On undisturbed plots seed rain was less than 20 million seeds per hectare. Increased seed rain was a result of increased plant cover and increased seed production per unit of cover. Seed rain on pinyon-juniper harvested plots had a large annual forb component as reported for other disturbed areas. Seed rain reflects the current successional stage and vigor of plants more than the climax community type.

Prediction of seed rain composition from general species floristics would be difficult. Seed rain and floristic composition were not in close agreement (SIV = 20% to 70%). The character of seed rain was determined by the relative cover of a few species producing a majority of the seed. A significant linear relationship existed for seed-producing species cover and its seed rain. But the proportion of perennial species contributing to seed rain was less than the proportion of annual species. The variability in annual populations reduces predictability of seed rain numbers and composition.

Similar seed rain composition on harvest and undisturbed plots (SIV = 47% to 70%) may in part explain the rapid reestablishment of predisturbance understory in the woodland. Reduced seed rain in undisturbed stands in part explains the previously reported decline in soil seed reserves as succession proceeds. Increased seed rain in the transition microsite reflects and perhaps maintains differences in understory distribution among soil microsites.

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SPECIES DIVERSITY AND HABITAT COMPLEXITY: DOES VEGETATION ORGANIZE VERTEBRATE COMMUNITIES IN THE GREAT BASIN?

David J. Germano[1] and David N. Lawhead[2]

ABSTRACT.—In this study, we have examined the effect of vegetation structure on the three major vertebrate taxa in Great Basin habitats of southwestern Utah. The effect of increasing vegetation heterogeneity, both horizontally and vertically, on the diversities of lizards, rodents, and postbreeding birds was investigated. We found no statistically significant relationship between diversity of all animal taxa and horizontal vegetation heterogeneity, although lizard diversity tended to decrease with increasing heterogeneity and rodent diversity tended to increase. Bird species diversity was positively correlated with vertical habitat heterogeneity. Abundances were highest for rodents in pinyon/juniper habitat and highest for lizards and birds in areas with the highest grass cover. Species richness was highest in sagebrush habitat for rodents but highest for lizards and birds in pinyon/juniper. Evenness values were relatively similar and high for birds and rodents and were relatively high for lizards in all habitats except for pinyon/juniper, which had an evenness value of 0.38. For rodents and lizards, abundance was significantly correlated with the index for horizontal habitat heterogeneity. After logarithmic transformation, abundance of lizards was positively correlated with increasing vegetation complexity. Combined abundance of lizards and rodents was also positively correlated with vegetation complexity. Rodent and lizard abundances, however, were affected by different aspects of the habitat. After logarithmic transformation, lizard abundances increased significantly with increasing grass cover, whereas rodent abundances increased significantly with increasing shrub cover.

Spatial heterogeneity, or simply the complexity of vegetation structure both horizontally and vertically, appears to predict species diversity in some instances, and many authors have felt that this is the primary factor causing differences in species diversity in communities (Pianka 1967, Rosenzweig and Winakur 1969, Karr 1971). MacArthur was the first to indicate that species diversity could be correlated with habitat diversity (MacArthur and MacArthur 1961, MacArthur et al. 1962). Others have found a similar trend of increasing animal diversity with increasing habitat complexity. This trend has been seen for birds (Karr 1971, Karr and Roth 1971, Tomoff 1974, Willson 1974, Lancaster and Rees 1979, Beedy 1981), lizards (Pianka 1966), rodents (Rosenzweig and Winakur 1969, Feldhamer 1979, Pizzimenti and De Salle 1981), and spiders (Hatley and MacMahon 1980).

By far the greatest amount of literature on this topic deals with the relationship between breeding bird communities and habitat complexity. This is the first study to consider (1) the relationship between vegetation complexity and postbreeding bird assemblages and (2) to consider more than one vertebrate class in an area. This allows us to ask several questions about species diversity and habitat complexity. Do postbreeding assemblages of birds conform to the pattern of increasing diversity with increasing habitat complexity seen for many breeding bird assemblages? Do diversities of several major taxa in the same habitats respond in the same way to vegetation structure? If measures of species diversity do not correlate with vegetation structure, are other measures of the relationship between a taxon and habitat more meaningful and predictive?

METHODS

Study Area

The study area is in the Escalante Desert of Utah, in the southeastern portion of the Great Basin (Fig. 1). We set up four 1,000 m transects in each of the five habitats that are the dominant vegetation types in this area. These habitats were uniform areas of pinyon/juniper, sagebrush, greasewood/shadscale, grassland, and an area we termed mixed shrub because it was a heterogeneous mix of small shrubs and grasses different from the other four habitats. These habitats generally followed an elevational gradient from approximately 1,550 to 1,785 m, with greasewood/

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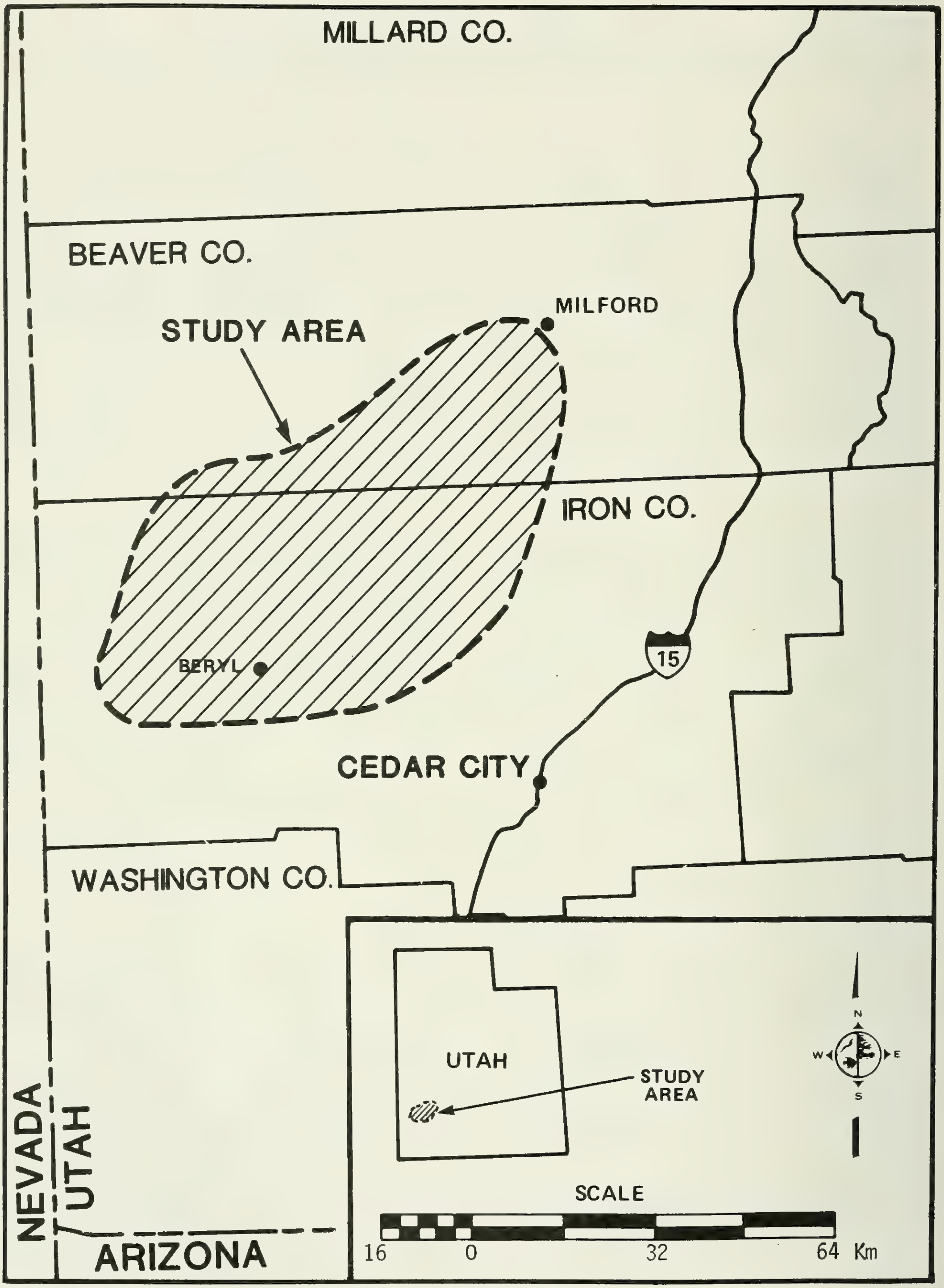
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Fig. 1. The study site in southwestern Utah in the Escalante Desert. Four 1,000 m transects were established in each of five Great Basin habitats within the shaded area.

shadscale in the valley bottom and pinyon/juniper woodland on the foothills of the mountain range bordering this valley. The other habitats were at intermediate elevations. This area is characterized by hot summer temperatures and cold winters. Annual rainfall averages approximately 200 mm, with precipitation falling in all months. The highest amount of precipitation falls in March and April, approximately 50 mm, 23% of the total. Each of the other months averages about 15 mm of precipitation, approximately 7% of total.

Field Methods

Five experienced investigators carried out censuses of rodents, lizards, and birds in July and August 1981. We used visual walking censuses to determine the densities of lizards and birds. We censused birds between 0530 and 0800 and lizards between 0900 and 1200. We recorded the species and number of animals sighted, distance of each observation from the transect line, and the compass direction of each observation. This information was entered into a computer program (Burnham et al. 1980) that gave a density estimate for each species. This method of line-transect sampling takes into account differential visibility of individual animals in different habitats. Where cover is more dense, the effective distance of sighting a bird or lizard is reduced. This, in turn, reduces the width of the area censused on either side of the transect line. A smaller belt of area on either side of the transect line gives a smaller area sampled for the number of observations and therefore corrects for decreased visibility. This computer program generates a different size of area censused for each species and for each habitat. Density estimates were, therefore, determined with visibility being an integral part of that estimate.

Rodents were live-trapped at night using the assessment line technique (O'Farrell et al. 1977) to determine rodent density. This technique also includes the movement behavior of the animal at the time of censusing in making density estimates. The assessment lines are trapping stations located perpendicular to the two main parallel lines of trapping stations. The assessment lines give a maximum boundary around the main census lines for each species by recording the farthest distance individuals of a species are caught from the main census lines. The length of the main census lines multiplied by the width, as determined by trapping on the assessment lines, gives an estimate of the area censused for each species.

Vegetation sampling was done using the Daubenmire Nested Quadrat method (Mueller-Dombois and Ellenberg 1974) on the same transects used to census animals. Sampling yielded plant species abundance, percent density, and percent cover.

Data Analysis

Species diversity and evenness values were calculated from the richness and abundance data using indices from Hill (1973). These indices define diversity as $N_2 = 1/\Sigma(p_i^2)$, where p_i is the relative abundance of the i^{th} species, and evenness as N_2/N_1, with $N_1 = \exp(-\Sigma p_i \ln p_i)$. The diversity index ($N_2$) expresses diversity with "species" as the basic unit and still includes an evenness component of species abundance pattern as well as richness. The diversity value calculated by this index is influenced more by the number and abundance of common species than rare species, although both are included in determining a diversity value. Hill (1973) points out that N_2 allows a more straightforward comparison among communities with different diversities and sample sizes (see Rotenberry 1978 for a summary of the advantages of using N_2 as a diversity index).

For vegetation we calculated indices for both horizontal and vertical heterogeneity. We determined horizontal heterogeneity using a habitat physiognomic complexity index (PCI) for each habitat type similar to that of Tomoff (1974). We determined this diversity index for each habitat again using the index N_2, where p_i equals the proportional cover value of each physiognomic component in the habitat (i.e., grass, cacti, forbs, shrubs, and trees). A habitat with only one or two of these components composing the majority of cover, or being the only components in the habitat, is not likely to have as much horizontal heterogeneity as a habitat that contains a somewhat equal mixture of components. We determined vertical heterogeneity using the Shannon-Weaver Information index, $H^2 = -\Sigma p_i \ln p_i$, to give foliage height diversity (FHD) where p_i is the proportion of the total cover of the foliage that lies in the i^{th} vertical layer

TABLE 1. Cover values (percent total cover) of physiognomic components and diversity indices for each habitat type. Habitats are listed in order of elevation from lowest to highest.

	Physiognomic component					Diversity index	
Habitat	Forb	Grass	Cactus	Shrub	Tree	PCI	FHD
Greasewood/ Shadscale	0.01	0.04	0	28.18	0	1.00	0.06
Mixed shrub	0.28	14.62	0.08	17.08	0	2.03	0
Grassland	0.48	14.06	0	12.97	0	2.07	0
Sagebrush	0.03	5.34	0.21	22.49	0	1.47	0.50
Pinyon/Juniper	0.31	1.12	0.02	3.95	22.02	1.50	0.61

TABLE 2. Species richness, abundance (number per hectare), evenness, and diversity of the three taxa for a gradient of habitats. The habitat types are listed in the order of their PCI value from highest to lowest. PCI values for each habitat are listed in parentheses below the habitat type.

	Habitat Type				
Taxon	Grassland (2.07)	Mixed shrub (2.03)	Pinyon/ Juniper (1.50)	Sagebrush (1.47)	Greasewood/ Shadscale (1.00)
LIZARDS					
Species richness	5	2	7	5	3
Abundance	27.87	22.12	4.25	8.69	4.43
Evenness	.69	.94	.38	.75	.86
Diversity	2.02	1.03	2.21	3.05	2.77
RODENTS					
Species richness	6	5	5	9	5
Abundance	2.66	6.22	18.32	8.01	11.36
Evenness	.84	.93	.96	.74	.72
Diversity	3.24	2.50	2.80	2.62	2.04
BIRDS					
Species richness	3	6	25	6	7
Abundance	8.96	1.95	3.19	0.22	1.21
Evenness	.94	.85	.70	1.00	.83
Diversity	1.92	3.39	8.67	4.79	3.21

(MacArthur and MacArthur 1961). Vegetation was divided into layers of 0 to 0.5 m, 0.5 to 1.0 m, and > 1.0 m. We used correlation and regression statistics to find relationships between PCI, FHD, and animal diversity.

RESULTS

Values of PCI for each habitat type were highest in the two habitats with abundant grass cover and lowest in the greasewood/ shadscale, where virtually all the cover was composed of similar-height shrubs (Table 1). The grassland and mixed shrub habitats had highest PCI values by virtue of having an even mix of two physiognomic components, whereas the other three habitats were dominated by only one physiognomic component. The pinyon/juniper habitat contained all five vegetation components, but only the tree category gave a significant cover value. Cover densities of forbs and cacti were low in all five habitats. Trees were present only in the pinyon/juniper habitat. However, values of FHD gave a different trend. The grassland and mixed shrub habitats, which gave the highest values for PCI, had values of 0 for FHD. Not too surprisingly, the highest value for FHD was for pinyon/juniper habitat.

For each animal taxon, the highest diversity indices occurred in different habitat types (Table 2). Birds showed the widest range in diversity values, with a high of 8.67 in pinyon/ juniper habitat and a low of 1.92 in grassland habitat. Diversities of rodents were the most similar, with a range of 2.04 to 3.24. Species richness was highest in the pinyon/ juniper for lizards and birds, but highest in the sagebrush for rodents. Birds also showed the widest range in species richness, with val-

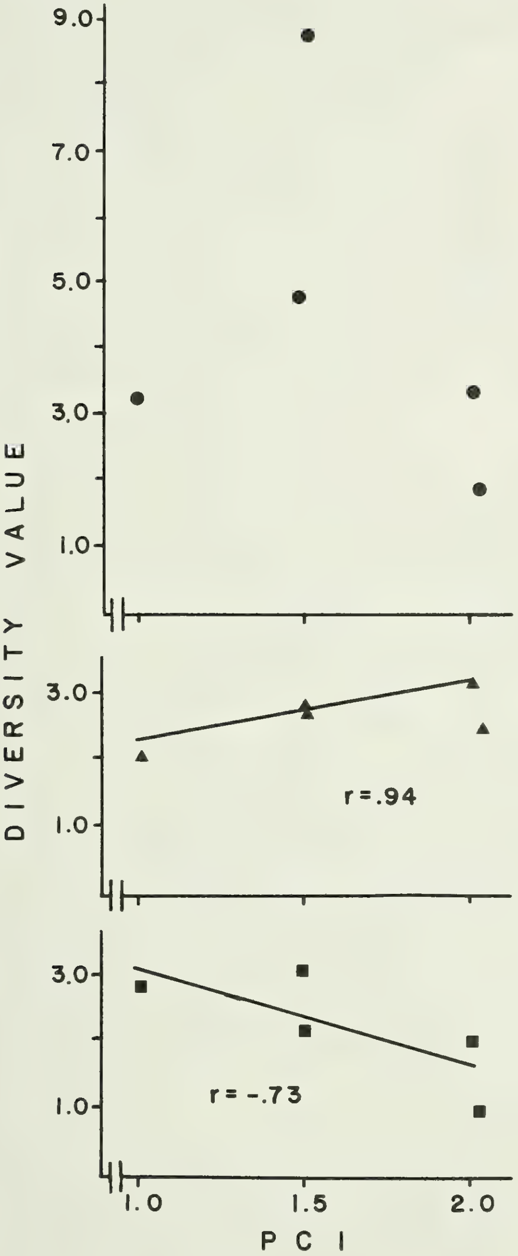

Fig. 2. Diversity values for birds (circles), rodents (triangles), and lizards (squares) versus the physiognomic complexity index (PCI) for five Great Basin habitats. Although the regression lines are not significant at the 0.05 level, trends are evident for lizards and rodents.

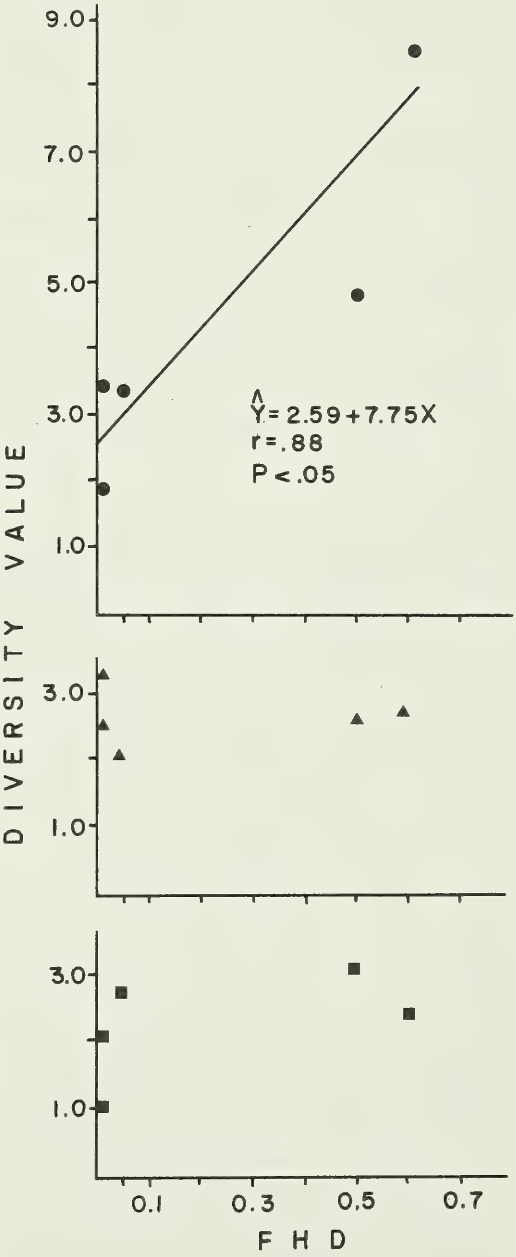

Fig. 3. Diversity values for birds (circles), rodents (triangles), and lizards (squares) versus foliage height diversity (FHD) for five Great Basin habitats. Lizards and rodents are not correlated to FHD, but postbreeding birds are significantly correlated.

ues from 3 to 25. Abundances were highest in the pinyon/juniper for rodents, but for birds and lizards they were highest in areas with abundant grass cover (Table 2, Appendices A, B, C). Although there is not a clear pattern, the areas with the lowest species richness produced the highest, or nearly the highest, abundance for each taxon. Evenness values were relatively high for birds and rodents in all habitats, ranging from 0.70 to 1.00 for birds

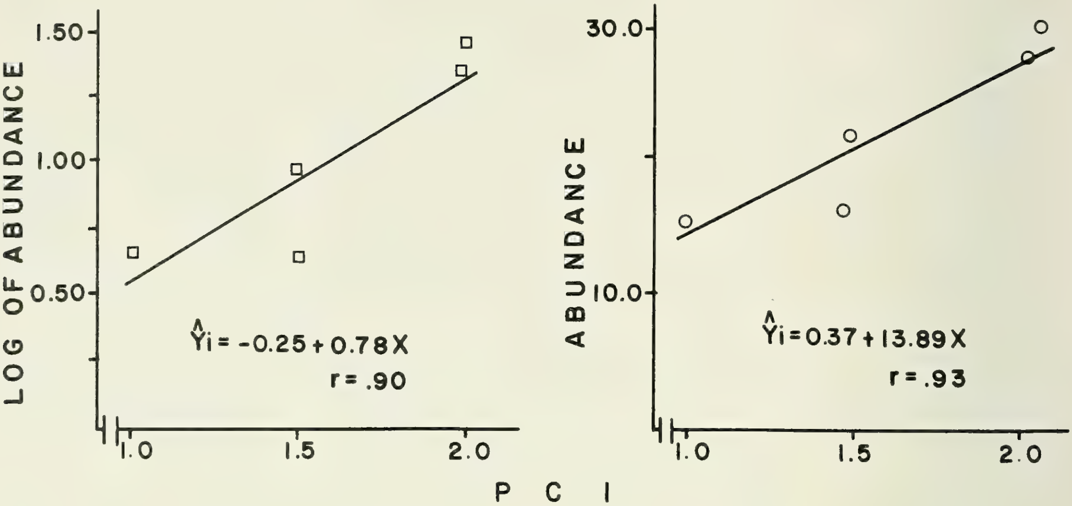

Fig. 4. The logarithmic transformation of lizard abundance (number per hectare) versus the physiognomic complexity index (PCI) for five Great Basin habitats on the left and the combined abundance (number per hectare) of rodents and lizards versus PCI for the same habitats on the right. Both regression lines are significant.

and 0.72 to 0.96 for rodents. For lizards, an unusually low evenness value of 0.38 was obtained for the pinyon/juniper habitat.

No statistically significant relationships came from plotting diversity indices for each taxon against PCI values for the five habitat types (Fig. 2), although rodent diversity was highly correlated to PCI and tended to increase with increasing PCI, and lizard diversity tended to decrease with increasing PCI. Bird diversity was positively correlated to FHD; lizard and rodent diversities were uncorrelated (Fig. 3). Although the relationships of diversity to horizontal habitat heterogeneity for rodents and lizards are suggestive, neither is statistically significant and therefore not wholly satisfying. We did find, however, that a component of diversity, abundance, was related to PCI in some instances. For lizards the logarithmic regression of abundance to PCI was significant and highly correlated, as was the regression of combined abundance for rodents and reptiles plotted against PCI (Fig. 4).

We looked at the above relationship more closely and found that lizard abundance increased with increasing grass cover. There is a significant ($P < .05$) negative relationship between percent grass cover and percent shrub and tree cover ($r = -.96$). As grass cover increased, there was a linear decline in overstory cover. Reptile abundance plotted against the ratio of percent grass cover over the percent shrub and tree cover gave a significant ($P < .01$) logarithmic relationship ($r = .98$, Fig. 5). As grass cover increased and overstory cover dropped, reptile abundance increased. We also found a significant ($P < .05$) inverse relationship between the logarithmic transformation of rodent abundance and the grass/overstory ratio ($r = -.91$ Fig. 5.) Rodent abundance decreased with increasing grass cover and increased with increasing shrub and tree cover. No pattern existed for bird abundances when plotted against the ratio of percent grass cover to percent shrub and tree cover.

DISCUSSION

In this part of the Great Basin, both lizard and rodent assemblages seem to be structured, at least in part, by the horizontal heterogeneity of the vegetation. Postbreeding bird assemblages are correlated with vertical heterogeneity.

For lizards there was a trend of decreasing diversity with increasing vegetation complexity. This trend is in contrast to the positive relationship Pianka (1966) found between the number of lizard species and plant volume diversity. Comparisons with this study are weak, however, because Pianka used species richness as his measure of animal diversity,

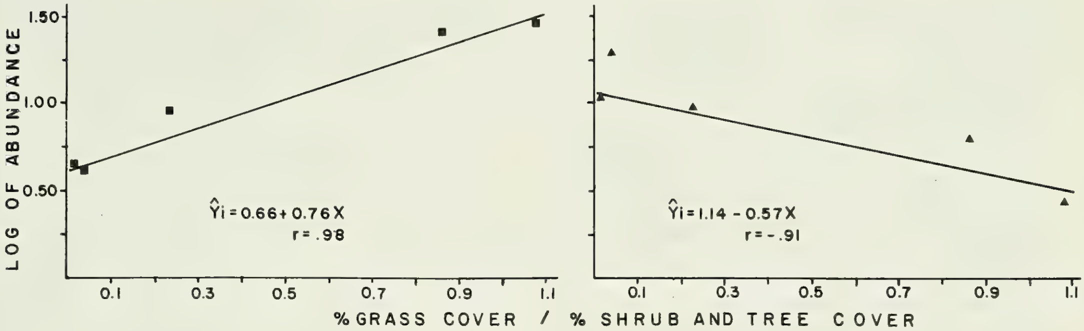

Fig. 5. The logarithmic transformation of lizard (squares) and rodent (triangles) abundances (number per hectare) versus the ratio of grass cover to shrub and tree cover in the five habitat types. Both regression lines are significant.

ignoring the abundance of each species. It should be noted that his vegetation complexity index is different from ours. The differences in these results may simply reflect the different indices used, although the number of lizard species we found in each habitat also did not correlate with vegetation complexity. We found that the abundance of lizards was significantly correlated with vegetation complexity and was positively correlated with an increasing percentage of grass cover in each habitat. This diverges from earlier findings by Germano and Hungerford (1981) in Sonoran desert grasslands, where relative abundance of reptiles was lowest in the area with the highest grass cover. Werschkul (1982), working in Great Basin habitat of Oregon, did not find any lizards in grassland habitat. Four of the five habitats we studied were numerically dominated by *Uta stansburiana*. In the two habitats with the highest lizard abundance, grassland and mixed shrub, *U. stansburiana* accounted for 68% and 98% of lizard abundance, respectively (Appendix A). In other areas that have been studied, *U. stansburiana* was not abundant in habitats with high grass cover (Fox 1978, Tinkle 1967, Werschkul 1982). Why was *U. stansburiana* most abundant in habitats with denser grass growth in the Escalante Desert? Fox (1982) found that juvenile *U. stansburiana* had better survival rates in habitats that are the most complex. In the area Fox studied, habitats that contained high grass cover were less complex, and this may be the general case in most areas; however, this is not the case in the Escalante Desert. Populations of *U. stansburiana* in the Escalante Desert may do better in these more horizontally heterogeneous habitats even though these habitats have the highest grass cover.

Rodents followed the opposite trend: diversity increased with increasing vegetation complexity. This general pattern was reported for rodents in the Sonoran Desert (Rosenzweig and Winakur 1969). Rodent abundance was also significantly correlated with increasing cover of shrubs and decreasing cover of grass. Pizzimenti and De Salle (1981) found that abundance of insectivorous rodents in Peru is positively correlated with increasing plant cover. They did not discuss the composition of plant communities, so it is not known if grass or shrubs were increasing the most in these areas. Much of the abundance of the overall rodent communities in our study was due to the abundances of species of *Peromyscus* and *Perognathus*. These species were found to be closely associated with shrubby vegetation (Rosenzweig and Winakur 1969) but, as Parmenter and MacMahon (1983) found, such vegetation may not be entirely necessary. When they experimentally removed shrubs from a plot in southwestern Wyoming, they found no change in population sizes, sex ratios, or age structure for several rodent species, including *Peromyscus maniculatus* and *Perognathus parvus*, both of which were found at our site.

Combining abundance of rodents and lizards gave us a significant positive relationship with horizontal habitat heterogeneity. It appears that horizontal heterogeneity benefits both lizards and rodents by increasing their collective abundance in a way seen for lizard abundance and habitat complexity but not seen for rodents when rodent abundance is considered alone. We do not know of a biological reason for this relationship in view of the fact that each taxon appears to occupy a different trophic level and each is separated in the habitat temporally.

Postbreeding bird diversity did not correlate with horizontal habitat heterogeneity (PCI) but did correlate with vertical habitat diversity (FHD) in our study area. The lack of correlation between horizontal vegetation complexity and either bird diversity or abundance was similar to the work by Wiens (1973, 1974a, 1974b) in western shrubsteppe habitats where no correlation between bird diversity and vegetation complexity could be found. Postbreeding bird assemblages in our study area did correlate with vertical layering, which was similar to the relationship seen for breeding bird assemblages in both tropical and temperate locales (MacArthur and MacArthur 1961, Karr 1971, Willson 1974, Lancaster and Rees 1979, Beedy 1981). This relationship appeared to hold wherever there was a significant range of vertical layering. It is not surprising, therefore, that the highest bird diversity was found in pinyon/juniper habitat, the only habitat with trees. Willson (1974) has previously indicated that adding trees in a vegetation series is important to increasing bird species diversity. We also found highest bird abundances in areas with highest grass cover, which is similar to the pattern of bird abundances in other grassland situations (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981).

The three major vertebrate taxa in this area appear to be structured differently in the same habitats. Postbreeding bird diversity is significantly correlated with vertical layering, but rodent and lizard diversities are correlated with horizontal habitat heterogeneity. These relationships could be expected given the plane of space in which these three taxa function. Many birds forage, nest, and roost in trees and therefore make greater use of vertical space than rodents or lizards. Rodents and lizards, on the other hand, are restricted more often to a horizontal plane of movement. If vegetation does structure rodent and lizard assemblages to some degree, then horizontal heterogeneity would likely act more strongly on their diversities, as this study has demonstrated. Statistically significant patterns for rodents and lizards appear only when the abundance of these taxa are considered. Abundances of lizards and rodents are closely correlated with the percent of grass and shrub cover in the five Great Basin habitats we studied.

ACKNOWLEDGMENTS

We thank John Wiens, Tom Fritts, Norm Scott, Edward Beedy, Ken Schoenly, and Sandy Mitchell for reading and critically evaluating various forms of this manuscript. Their efforts helped focus our writing. We also thank Bob Whitmore, Jeanne Conry, and Bruce Webb for assistance in the field. Melissa Mooney and Jeff Soto collected the vegetation data and for this we thank them. Tom Mulroy deserves special thanks for initial encouragement and support of this study. Financial support for this study was provided by HDR Sciences, Inc., through a contract from the U.S. Air Force.

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APPENDIX

TABLE A. Reptile density (number per hectare), by habitat type, in Great Basin habitats of the Escalante Desert, Utah.

	Habitat type				
Species	Pinyon/ Juniper	Sagebrush	Grassland	Mixed shrub	Greasewood/ Shadscale
Crotaphytus insularis	0	0.35	0	0	0
Gambelia wislizenii	0.50	1.04	3.80	0	0
Sceloporus occidentalis	0.25	0	0	0	0
S. graciosus	0	0.35	0	0	2.22
Uta stansburiana	1.75	4.52	19.01	21.74	1.33
Phrynosoma platyrhinos	0.25	0	1.90	0	0
P. douglassi	0.25	0	0.63	0.38	0.44
Cnemidophorus tigris	0.75	1.04	0.63	0	0
Unidentified lizard	0.25	1.39	1.93	0	0.44
Masticophus taeniatus	0.25	0	0	0	0
Species richness	7	5	5	2	3
Abundance	4.25	8.69	27.87	22.12	4.43

TABLE B. Rodent density (number per hectare), by habitat type, in Great Basin habitats of the Escalante Desert, Utah.

	Habitat type				
Species	Pinyon/ Juniper	Sagebrush	Grassland	Mixed shrub	Greasewood/ Shadscale
Dipodomys microps	0	0	0	0	1.02
D. ordii	0	0	0.01	0	1.53
D. sp.	0	0.01	0	0	0
Perognathus formosus	0.71	0	0.41	2.69	0
P. parvus	0	0.85	0	0.76	0
P. longimembris	0	0.01	1.19	2.77	0

Table B continued.

	Habitat type				
Species	Pinyon/ Juniper	Sagebrush	Grassland	Mixed shrub	Greasewood/ Shadscale
Microdipodops megacephalus	0	1.36	0	0	0
Peromyscus maniculatus	7.24	4.57	0.58	0.01	7.70
P. truei	7.98	0.96	0.01	0	0
P. boylii	0	0.01	0	0	0
P. eremicus	0	0	0	0	0.63
Onychomys leucogaster	0	0.27	0.48	0	0.48
Eutamias dorsalis	1.60	0	0	0	0
Neotoma lepida	0.79	0	0	0	0
Ammospermophilus leucurus	0	0.01	0.01	0.01	0
Species richness	5	9	6	5	5
Abundance	18.32	8.01	2.66	6.22	11.36

TABLE C. Bird density (number per hectare), by habitat type, in Great Basin habitats of the Escalante Desert, Utah.

	Habitat type				
Species	Pinyon/ Juniper	Sagebrush	Grassland	Mixed shrub	Greasewood/ Shadscale
Accipiter cooperii	0.02	0	0	0	0
Zenaida macroura	0.20	0.03	3.18	0	0
Chordeiles minor	0	0	0	0	0.01
Aeronautus saxatalis	0	0.01	0	0	0
Colaptes auratus	0.02	0	0	0	0
Picoides villosus	0.04	0	0	0	0
Myiarchus cinerascens	0.14	0	0	0	0
Empidonax wrightii	0.02	0	0	0	0
Eremophila alpestris	0.29	0.01	5.63	0.79	0.52
Aphelocoma coerulescens	0.04	0	0	0	0
Gymnorhinus cyanocephalus	0.04	0	0	0	0
Parus inornatus	0.45	0	0	0	0
Psaltriparus minimus	0.18	0	0	0	0
Thyromanes bewickii	0.23	0	0	0	0
Mimus polyglottos	0.04	0	0	0	0
Oreoscoptes montanus	0.02	0	0	0.09	0.04
Sialia currucoides	0.02	0	0	0	0
Polioptila caerulea	0.02	0	0	0	0
Lanius ludovicianus	0.02	0	0	0.02	0.01
Vireo vicinior	0.02	0	0	0	0
Dendroica nigrescens	0.08	0	0	0	0
Sturnella neglecta	0	0	0.09	0	0
Carpodacus mexicanus	0.06	0	0	0	0
Loxia curvirostra	0.04	0	0	0	0
Pipilo erythrophthalmus	0.02	0	0	0	0
Chondestes grammacus	0.04	0	0	0	0
Amphispiza bilineata	0.78	0.05	0	0.11	0.05
A. belli	0	0.04	0	0.34	0.21
Spizella passerina	0.33	0	0	0	0
S. breweri	0	0	0	0.60	0.37
Unidentified	0.04	0.07	0.06	0	0
Species richness	25	6	3	6	7
Abundance	3.19	0.22	8.96	1.95	1.21

COMPARISON OF INSECTS FROM BURNED AND UNBURNED AREAS AFTER A RANGE FIRE

James D. Hansen[1]

ABSTRACT.—Insect communities at recently burned and unburned sites in the Great Basin of northwestern Utah were studied by weekly sampling with pitfall and Malaise traps. More specimens were consistently collected at the burned site, although the numbers of species between the sites were about equal a month after the fire. Flying insects showing no preference for the sites were sciarids, phorids, and leafminer flies (all Diptera). Insects preferring the unburned site were mostly entomophagous flies such as pipunculids, chamaemyiids, and tachinids. Insects more common at the burned site were mosquitoes and phytophagous species of lygaeid bugs, leafhoppers, and moths. Seasonal trends in relative abundance of major families of flying insects are reported. Ground survivors included gryllacridids, carabids, tenebrionids, and ants. Silphids and buprestids immigrated into the burned area soon after the fire. Interrelationships between the burned area and the insect community are dicussed.

Fire is an important component of the rangeland ecosystem in the western United States. By consuming excess organic material, range fires release nutrients for future growth, stimulate regrowth of preferred forage species, and eliminate undesired plants. In many areas, repeated burnings perpetuate grasslands.

The effect of range fires on resident insect communities, however, is poorly known. Most of the previous research on the relationship between fire and insects were from the midwest. Rice (1932) studied the influence of fire on animals, including insects, in an Illinois prairie. Cancelado and Yonke (1970) reported the effect of prairie fire on insects in Missouri. Several studies on prairie burns and insect populations were conducted in Kansas (Nagel 1973, Knutson and Campbell 1976, Evans et al. 1983, Seastedt 1984).

The present study sought to ascertain insect survival immediately after a range fire in the Great Basin and detect immigration of the first potential phytophagous colonizers. Secondary objectives were to assess the immigration of predaceous and parasitic insects after a fire, and to determine the seasonal activity of adults of major insect groups in typical burned and unburned areas.

MATERIALS AND METHODS

The study area was in Box Elder County, Utah, north of the Great Salt Lake between the Wildcat Hills and the Raft River Mountains. Elevation was between 1,340 and 1,460 m. Predominant native plants were big sagebrush, *Artemisia tridentata* Nutt.; winterfat, *Ceratoides* sp.; rabbitbrush, *Chrysothamnus* sp.; and western wheatgrass, *Pascopyrum smithii* (Rydb.) Löve. Major introduced species were cheatgrass, *Bromus tectorum* L.; crested wheatgrass, *Agropyron* spp.; and intermediate wheatgrass, *Thinopyrum intermedium* (Host).

On 7 July 1983 lightning started a range fire that burned at least 20,000 contiguous hectares. The fire, fueled by senescent cheatgrass, was hot enough to destroy most of the sagebrush cover.

The unburned (comparison) site, 24 km west of Snowville, Utah, was established on 20 May 1983 in an old plot (ca one hectare) of intermediate wheatgrass surrounded by sagebrush and rabbitbrush.

The burned site, ca 11 km south of the unburned site and at least 3 km within the boundary of the burn, was similar in slope and elevation to the unburned site. Insects were first sampled a week after the fire. Notes on revegetation were recorded during the season.

Insects were collected by two methods. Malaise traps, used for flying insects, were made of off-white polyester marquisette ma-

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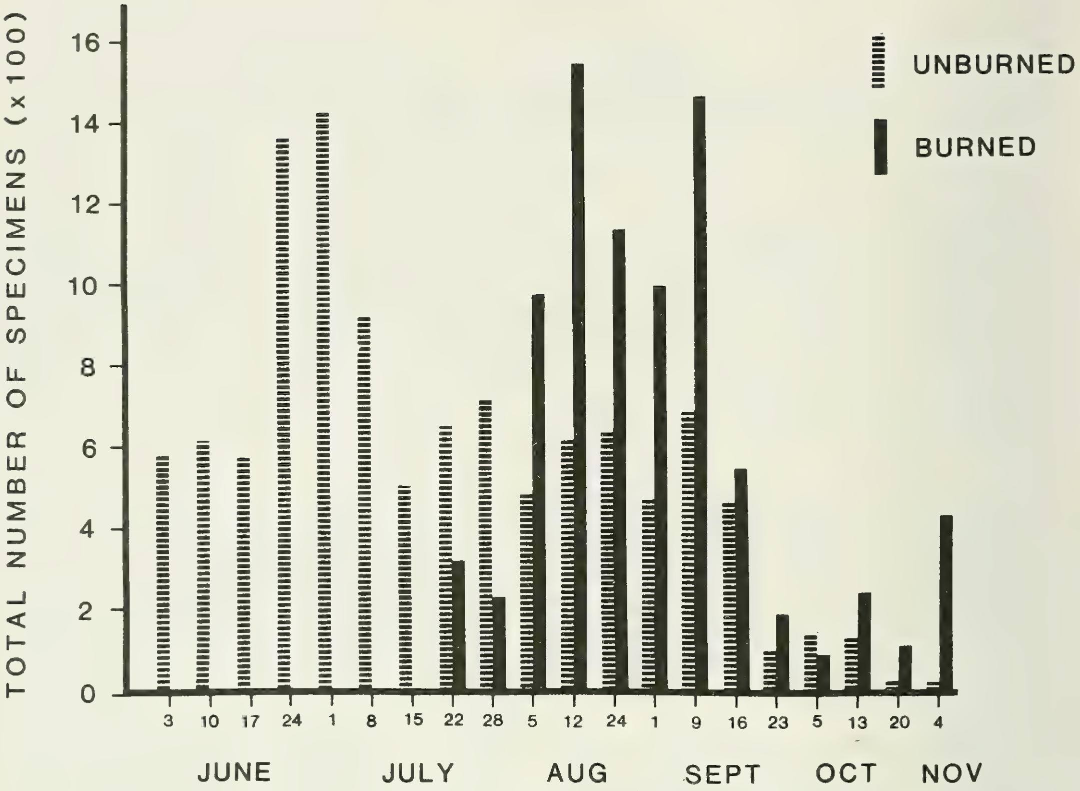

Fig. 1. The number of specimens in weekly Malaise trap collections from unburned site and burned sites in Box Elder County, Utah, during 1983.

terial, square in configuration with four central vanes, and each topped with a clear acrylic collecting tube. The traps were purchased from BioQuip Products (P. O. Box 61, Santa Monica, California 90406).[2] A trap was placed in the grassy area of the unburned site and another at the burned site.

Pitfall traps were used to sample ground inhabiting insects. The trap, similar to that described by Morrill (1975), was composed of a 4-oz plastic cup that collected specimens that fell through a funnel made of a 7-oz tapered plastic cup with the bottom cut out. This whole unit was housed in a 16-oz plastic cup and buried to surface level. At the unburned site, seven traps were arranged on a linear transect ca 20 m apart in the shrubby area; additional pitfalls were placed under and near the Malaise trap. At the burned site, 10 traps were ca 10 m apart along a linear transect near the Malaise trap.

Specimens from Malaise and pitfall traps were collected weekly from the establishment of study sites until 4 November 1983. Collections were not made during the weeks of 19 August and 27 October because of severe rain.

Insects were identified at least to the family level and separated by morphospecies (Janzen and Schoener 1968, Allan et al. 1975). Genus and, when possible, species were determined for abundant specimens. Moths could not be segregated into families because of the poor condition of samples from the Malaise traps.

RESULTS

Althought the fire severely damaged vegetation, regrowth was evident by 29 July. In early September cheatgrass was plentiful and averaged ca 5 mm in height; sagebrush and rabbitbrush also recovered. In the following months, western wheatgrass became the dominant grass for the remaining sampling period.

Collection data from the Malaise traps showed that the number of specimens col-

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[2] Mention of trade name is for identification only and does not imply an endorsement to the exclusion of other products that may be suitable.

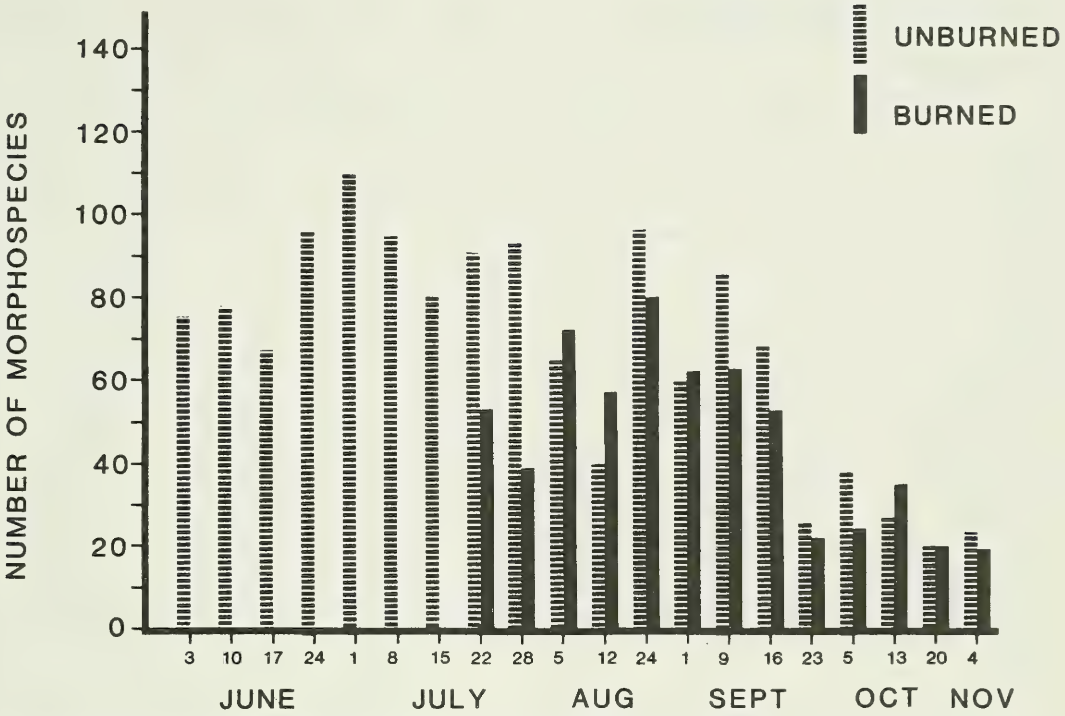

Fig. 2. The number of morphospecies identified from weekly Malaise trap collections either from an unburned site or a burned site in Box Elder County, Utah, during 1983.

lected at the unburned site peaked during the last two weeks in June and was higher than the burned site in the first two collections after the fire (Fig. 1). More specimens were consistently collected at the burned site, with the greatest amount in August and September. Numbers declined from mid-September through the fall.

Nearly all the specimens collected by the Malaise traps were adults from the winged orders (Homoptera, Hemiptera, Lepidoptera, Diptera, and Hymenoptera). Abundant families, however, were arranged by species. The number of species collected at the unburned site remained about the same before and three weeks after the fire (Fig. 2). Similar numbers of species were then collected at the burned site from August onward. Numbers at both sites decreased during fall.

To determine site preference, the collection data were grouped taxonomically. Most specimens were sorted to family only because of insufficient numbers at the morphospecies level. Abundant families, however, were arranged by species. Although Malaise traps were not intended to measure population density, they do indicate relative abundance. Major families, determined by the number of specimens, were grouped into three classes: those showing no preference or those clearly preferring either of the sites. Hymenoptera were clumped into two groups. Parasitic Hymenoptera contained Braconidae, Ichneumonidae, Mymaridae, Eulophidae, Encyrtidae, Eupelmidae, Eucharitidae, Pteromalidae, Eurytomidae, Chalcididae, Proctotrupidae, Ceraphronidae, Diapriidae, Scelionidae, Chrysididae, Bethylidae, Dryinidae, Tiphiidae, and Mutillidae. Predaceous Hymenoptera contained mainly pompilid and sphecid wasps.

Insects having no site preference were Sciaridae (mostly *Lycoriella* spp.), four unidentified species of Phoridae, 16 species of Agromyzidae, and many parasitic Hymenoptera (Table 1). Those preferring the unburned site were 15 species of Bombyliidae, 3 species of Pipunculidae (most were *Pipunculus* sp. and *Prothecus* sp.), 6 species of Chamaemyiidae, and 39 species of Tachinidae (with *Hyalomya aldrichii* Townsend and *Paradidyma singularis* Townsend the most

TABLE 1. Insects having no preference between unburned and burned sites in Box Elder County, Utah, during 1983 as shown by weekly Malaise trap collections.

Collection date	Sciaridae	Phoridae	Agromyzidae	Parasitic[1] Hymenoptera
3 June	67[2]	68	67	26
10 June	55	31	9	28
17 June	5	15	20	38
24 June	7	57	72	18
1 July	70	48	58	74
8 July	53	113	39	159
15 July	11 (0)	74 (0)	0 (0)	34 (0)
22 July	16 (2)	88 (2)	43 (3)	38 (8)
28 July	6 (11)	125 (3)	97 (4)	20 (0)
5 August	0 (0)	109 (48)	12 (10)	11 (14)
12 August	0 (0)	45 (140)	0 (0)	5 (8)
24 August	0 (9)	109 (60)	7 (12)	11 (11)
1 September	6 (6)	19 (36)	17 (46)	6 (39)
9 September	80 (65)	56 (25)	9 (23)	29 (29)
16 September	44 (5)	22 (41)	1 (6)	42 (7)
23 September	1 (6)	0 (0)	11 (2)	8 (4)
5 October	19 (12)	0 (0)	0 (0)	17 (11)
13 October	37 (45)	0 (0)	1 (0)	7 (76)
20 October	3 (3)	1 (2)	0 (0)	9 (19)
4 November	4 (175)	1 (4)	1 (1)	6 (202)

[1] Parasitic Hymenoptera are Braconidae, Ichneumonidae, Mymaridae, Eulophidae, Encyrtidae, Eupelmidae, Eucharitidae, Pteromalidae, Eurytomidae, Chalcididae, Proctotrupidae, Ceraphronidae, Diapriidae, Scelionidae, Chrysididae, Bethylidae, Dryinidae, Tiphiidae, and Mutillidae.

[2] Data from burned site are in parentheses; otherwise, data are from unburned site.

common) (Table 2). Insects that preferred the burned site were Lygaeidae (almost all were the false chinch bug, *Nysius raphanus* Howard, plus some western bigeyed bugs, *Geocoris pallens* Stål), 31 species of Cicadellidae (dominated by *Empoasca aspera* Gillette & Baker, *Dikraneura carneola* [Stål], and *Parabolocratus viridis* Uhler), moths (mainly *Euxoa* spp., other Noctuidae, and microlepidopterans), three species of Culicidae [*Aedes dorsalis* (Meigen), *Culiseta inornata* (Williston), and *Culex tarsalis* (Coquillett)], and two families of predaceous wasps (Pompilidae and Sphecidae) (Table 3).

Specimens of certain families were collected in sufficient numbers to denote seasonal trends in adult abundance. Leafhoppers (Table 3) reached the highest levels at the end of June, decreased throughout the summer, but then increased at the burned site during the first week of September. Bombyliids (Table 2) were very rare until August, when numbers increased dramatically at the unburned site and remained at abundant levels through the first part of September. Phorids (Table 1) generally maintained their highest levels at the unburned site through July and August, although fewer were collected at the other site during this period. Chamaemyiids (Table 2) increased rapidly through July to peak at the end of August, then were gone by the end of September. Agromyzids had the highest peak in late July at the unburned site, then another lesser peak at the burned site during the last week of August.

Flying insects collected from pitfall traps were disregarded and only ground dwellers recorded. Specimens from the first collection at the burned site included *Stenopelmatus fuscus* Haldeman (Orthoptera: Gryllacrididae), several species of carabids, *Acmaeodera immaculata* Horn (Coleoptera: Buprestidae), some tenebrionids (mainly *Eleodes* spp.), and ants. Silphids (mostly *Nicrophorus* spp.) were taken two weeks later. All except *S. fuscus* and *A. immaculata* were also collected at the unburned site.

DISCUSSION

Malaise traps were not designed to accurately estimate population densities. The traps are valuable, however, in detecting relative abundance, seasonal changes in numbers, species diversity, and flight activity and efficiently obtaining specimens of major pterygote orders (Evans and Owen 1965, Matthews and Matthews 1971). Cancelado

TABLE 2. Insects preferring the unburned site in Box Elder County, Utah during 1983 as shown by weekly Malaise trap collections.

Collection date	Bombyliidae	Pipunculidae	Chamaemyiidae	Tachinidae
3 June	6[1]	6	1	7
10 June	4	4	0	21
17 June	0	4	1	6
24 June	3	4	1	11
1 July	0	2	1	21
8 July	2	0	0	13
15 July	2 (0)	15 (0)	2 (0)	7 (0)
22 July	3 (0)	103 (0)	19 (2)	36 (3)
28 July	8 (1)	78 (0)	0 (0)	12 (5)
5 August	9 (0)	30 (0)	30 (3)	7 (17)
12 August	32 (2)	34 (0)	0 (0)	97 (2)
24 August	24 (17)	10 (0)	43 (2)	28 (56)
1 September	18 (2)	16 (0)	0 (1)	95 (26)
9 September	18 (5)	19 (0)	1 (4)	64 (15)
16 September	4 (2)	55 (0)	21 (1)	61 (17)
23 September	0 (0)	1 (1)	1 (0)	9 (8)
5 October	0 (0)	3 (0)	0 (0)	13 (4)
13 October	0 (0)	0 (0)	0 (0)	2 (3)
20 October	0 (0)	0 (0)	0 (0)	0 (0)
4 November	0 (0)	1 (0)	0 (0)	0 (0)

[1] Data from burned site are in parentheses; otherwise, data are from unburned site.

and Yonke (1970) used Malaise traps to measure taxonomic differences in insect communities between burned and unburned areas of a Missouri prairie.

Malaise trap data from the unburned site showed seasonal patterns of adult insects (Fig. 2). Although more species were found at the end of June, the number of species fluctuated moderately at both sites, then decreased in mid-September. Seasonal environmental changes influenced species abundance. Grasses completed flowering by July and started senescing later that month, thus reducing the food supply for grass-feeding insects. Rabbitbrush, which started to bloom at the end of August and retained flowers until mid-October, provided food for many insects during the last part of the season. Evans and Murdoch (1968), by sampling a Michigan grassland with sweep nets and a Malaise trap, related the period of maximum species to the greatest availability of flowers. Food sources required to maintain the species richness level during midsummer were not apparent.

The largest weekly collections were from the burned site (Fig. 1). Many specimens were potential herbivorous colonizers (Table 3). Large numbers of false chinch bugs, which attack forbs and shrubs, may characterize areas disturbed by fire. In the same year as this study, I observed high densities of false chinch bugs (estimated at greater than 200 insects/m^2) after a large range fire (ca 4,400 ha) in Skull Valley, Utah. Cancelado and Yonke (1970) also reported collecting significantly more lygaeids from a burned area, but they did not identify the species.

Most leafhoppers were found just before the fire; numbers peaked again at the burned site the first week of September. At their grassland site, Murdoch et al. (1972) collected the largest number of Homoptera in June and July and found that insect diversity was highly correlated with both plant diversity and plant structure. Hawkins and Cross (1982), however, found no correlation between plant community parameters and insect diversity on reclaimed coal mine spoils in Alabama even though insect species richness seemed related to the densities of several plant species.

After the fire, more leafhoppers were collected from the burned site; other researchers reported similar observations (Cancelado and Yonke 1970, Nagel 1973). Major leafhoppers *D. carneola* and *P. viridus* were probably grass feeders (Thomas and Werner 1981), whereas *E. aspera* probably attacked forbs and shrubs. Hewitt and Burleson (1976) frequently found *D. carneola* on unburned rangeland in Montana.

TABLE 3. Insects preferring the burned site in Box Elder County, Utah, during 1983 as shown by weekly Malaise trap collections.

Collection date	Lygaeidae	Cicadellidae	Lepidoptera	Culicidae	Predaceous[1] Hymenoptera
3 June	0[2]	27	42	0	0
10 June	0	122	93	0	0
17 June	1	208	104	0	0
24 June	4	881	34	0	0
1 July	2	922	24	2	1
8 July	2	234	38	4	1
15 July	4 (0)	194 (0)	18 (0)	0 (0)	6 (0)
22 July	0 (0)	145 (19)	34 (94)	1 (123)	4 (6)
28 July	4 (2)	122 (56)	91 (2)	3 (94)	11 (0)
5 August	15 (324)	73 (203)	23 (174)	0 (7)	2 (33)
12 August	67 (1040)	100 (63)	101 (98)	0 (0)	3 (42)
24 August	148 (451)	53 (239)	36 (134)	1 (9)	3 (16)
1 September	37 (91)	94 (127)	43 (481)	61 (77)	1 (6)
9 September	154 (263)	107 (291)	40 (445)	19 (239)	8 (2)
16 September	36 (153)	79 (95)	33 (129)	6 (48)	2 (6)
23 September	10 (33)	23 (54)	9 (60)	1 (0)	0 (1)
5 October	11 (25)	25 (20)	2 (5)	0 (1)	0 (0)
13 October	21 (49)	11 (2)	5 (17)	0 (2)	0 (0)
20 October	1 (44)	1 (2)	2 (5)	0 (9)	0 (0)
4 November	1 (5)	0 (2)	2 (3)	0 (9)	0 (0)

[1] Predaceous Hymenoptera are Pompilidae and Sphecidae.

[2] Data from burned site are in parentheses; otherwise, data are from unburned site.

Many of the moths taken at the burn site were *Euxoa* spp. The larvae, called cutworms, have a wide host range yet are rarely encountered because they inhabit soil.

Agromyzids were common at both sites (Table 1). They are an important component of rangeland because their larvae mine leaves and stems of grasses, forbs, and shrubs. Yet, agromyzids were at the burn site even though vegetation was poorly developed when the flies were collected.

Parasitic hymenopterans were regularly collected at both sites. Chalcids were never abundant, yet they represented ca 30 species in eight families. Mutillids, external parasites of larvae and pupae of various wasps and bees, were collected more often at the burned site. Later in the season, braconids and ichneumonids also were more common at the burned site; they parasitize caterpillars, beetle and sawfly larvae, maggots, various bugs, aphids, spiders, and other wasps. Other hymenopterans more abundant in the burned site were pompilids, which are spider-hunting wasps, and sphecids, which are predators of aphids, bugs, grasshoppers, planthoppers, leafhoppers, flies, caterpillars, beetles, bees, and spiders. Adults of all these entomophagous wasps are attracted to flowers. Flowers, prey, and potential hosts presumably were scarce at the burned site, yet wasps were common there.

Pipunculids were found only at the unburned site (Table 2). Their larvae are solitary internal parasites of nymphs and adults of Homoptera, particularly leafhoppers. Nevertheless, the burned site Malaise trap collections contained many potential hosts. Pipunculid biology, however, is poorly known and factors other than food supply may have influenced the flies to avoid the burned area. These flies may be good indicators of undisturbed areas because they were consistently absent from the burned site.

Cursorial insects were collected with pitfall traps. Although pitfall traps are limited in effectiveness (Greenslade 1964, Luff 1975), they have been successfully used to collect and compare surface arthropods from different sites (Fitcher 1941, Morrill 1975). The traps indicate that ants and ground-dwelling beetles survived the fire, probably escaping the heat by being below the ground surface. The fire did not destroy all organic material, such as brome seeds, so that food resources were available for ants to maintain their colonies and for the polyphagous beetles. Other studies have verified that ground insect populations are unharmed by fire or changes in vegetative architecture. Rice (1932) collected more ants on burned prairie in Illinois than on nearby control sites. Removal of shrubs from a shrub-steppe site in Wyoming did not adversely affect the abundance of tenebrionids and carabids (Parmenter and MacMahon 1984).

The collection data suggested that *A. immaculata* is attracted to stressed environments because specimens were only found in pitfall traps on the burned site. Many buprestid species are sensitive to smoke and heat, and the beetles may have been attracted by volatiles from burned winterfat, the host plant for the larvae. Furthermore, larvae may survive by feeding on the roots of damaged plants.

Pitfall traps commonly collected two other types of insects. Silphids may have entered pitfall traps to feed on the dead bodies of other insects. No apparent reason explained why the omnivorous Jerusalem crickets, *S. fuscus*, were not collected at the unburned site.

The present study raises several questions about the relationship between fire and the insect community. For example, why were so many predaceous and parasitic hymenopterans in the burned area (Table 3), especially when so few flowers and, presumably, potential hosts were present? Why did parasitic flies avoid the burned site that contained abundant potential hosts? Some groups, particularly leafhoppers and moths, apparently are attracted to burned areas, but unfortunately their means of orientation are not well known. Although only adults were examined in this study, this is the main life stage at which many insects disperse into various habitats.

Although fire is a common management tool for rangeland, this study raises important considerations of its use. Herbivorous insects seem very attracted to burned sites, yet their natural enemies, particularly parasitic flies, avoid those locations. Consequently, vegetative regrowth is highly susceptible to plant feeders and may be so severely stressed as to inhibit stand reestablishment. The abundance of insect herbivores also presents a danger to reseeding programs. Young vegetation is often highly susceptible to insect herbivory. Obviously, more research is needed to determine the long-term effects of range fires on insect and plant communities.

ACKNOWLEDGMENTS

Appreciation is extended to: D. C. Nielson, C. L. Nowak, and S. F. Parker for their assistance; W. J. Hanson, G. E. Bohart, and F. D. Parker for identifying specimens; and USDI, Bureau of Land Management for use of study sites.

This research was the result of cooperative investigations of the USDA-ARS and the Utah Agricultural Experiment Station, Logan, Utah 84322. Approved as Journal Paper No. 3027.

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SIZE, STRUCTURE, AND HABITAT CHARACTERISTICS OF POPULATIONS OF *BRAYA HUMILIS* VAR. *HUMILIS* (BRASSICACEAE): AN ALPINE DISJUNCT FROM COLORADO

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ABSTRACT.—Size, structure, and habitat characteristics were studied in three populations of *Braya humilis* var. *humilis* (C. A. Meyer) Robins. in Gray & Wats. (Brassicaceae), a small, herbaceous perennial of the alpine tundra in central Colorado. There was a significant association between numbers of reproductive, juvenile, and seedling individuals and population location. Plant size within reproductive, juvenile, and seedling size classes varied significantly among three populations. Plots containing *Braya* had significantly lower total plant cover, a different set of dominant plant species, more rock, bare ground, and less litter than plots without *Braya*. *Braya* appears to be restricted to calcareous substrates that experience a moderate level of disturbance, such as solifluction lobes and abandoned roads. Populations are small despite the existence of much potential habitat. Population studies are necessary for active conservation management of *Braya*.

Braya humilis var. *humilis* (C. A. Meyer) Robins. in Gray & Wats. (Brassicaceae) is a small, herbaceous perennial that occurs in the alpine tundra of the Rocky Mountains in central Colorado. It is a rare taxon, disjunct from its nearest relatives in Canada by approximately 1,600 km. The isolated populations in Colorado were previously treated by Rollins (1953) as *B. humilis* ssp. *ventosa*. However, recent monographic work by Harris (1985), based on greenhouse and common garden studies, indicates that the Colorado plants should be treated with *B. humilis* var. *humilis*. In North America *Braya humilis* var. *humilis* occurs from Alaska, south through the northern Rocky Mountains to Alberta and British Columbia, north through the western Canadian Arctic Archipelago, east to Greenland, Newfoundland, Anticosti Island, Vermont, and the north shore of Lake Superior (Harris 1985). Colorado populations of *B. humilis* may represent isolated relicts left behind on small areas of calcareous alpine habitat as glaciers retreated about 12,000 years before present (Harris 1985). Hereinafter, *Braya* will refer to *Braya humilis* var. *humilis*.

In Colorado, *Braya* is restricted to calcareous soils derived from Paleozoic rock formations such as the Mississipian Leadville Limestone and Ordovician Manitou Dolomite (Tweto 1974). The plant commonly grows in association with *Dryas octopetala, Carex rupestris,* and *Kobresia myosuroides* on exposed slopes without late-lying snowbanks. It is often found growing in solifluction lobes, on low-angle scree slopes, and on gravel with minor amounts of soil movement, but it also grows on man-made disturbances such as old mining roads and prospects.

In Colorado, *Braya* is known to exist only in 19 small isolated populations at 12 general locations in the Mosquito, Ten Mile, Elk, and Collegiate ranges. At nearly all of its known occurrences in Colorado, *Braya* populations are small despite the existence of much apparent potential habitat. Approximately 3,900 individuals exist in Colorado, based on estimates for each known population. It is a taxon of special concern in Colorado (O'Kane 1986) and is currently a candidate for listing (Category 2) by the U.S. Fish and Wildlife Service under the Endangered Species Act (Fay 1985).

Counts of one population west of Hoosier Pass, Colorado, have varied greatly, suggesting considerable year-to-year fluctuation in numbers (Harmon 1980, Johnston 1984, Neely 1985). Unfortunately, the accuracy of these counts is questionable because the plants are small and easily overlooked. Accurate counts are important for determining the size and dynamics of populations and are fun-

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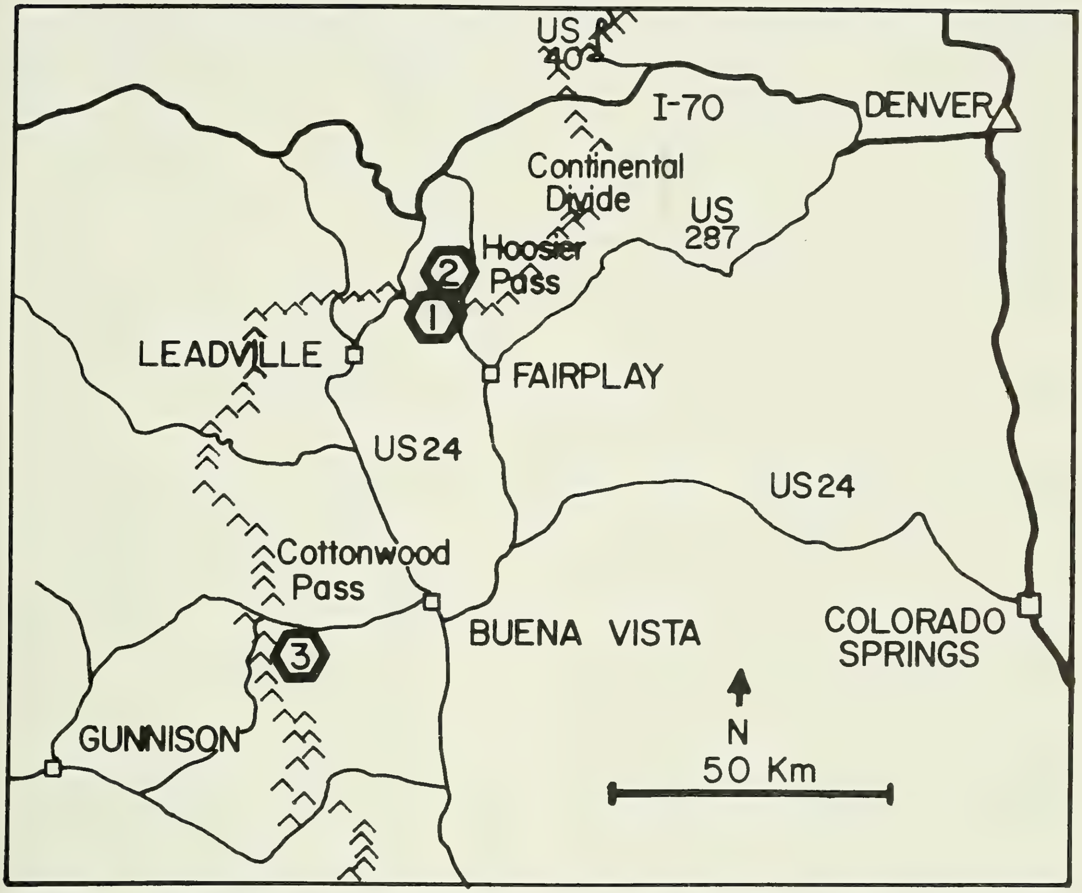

Fig. 1. Locations of the three study sites in central Colorado. 1 = Mt. Bross, 2 = West Hoosier, and 3 = Spout Lake.

damental to the conservation management of the taxon (Bradshaw and Doody 1978).

Relatively few population studies have been undertaken on long-lived perennials, particularly those that are rare. There is increasing recognition by plant conservationists of the need to monitor rare plant populations to determine population structure, flux, and modes of population regulation (Bradshaw and Doody 1978, Whitson and Massey 1981, Kruckeberg and Rabinowitz, unpublished manuscript).

We initiated in 1985 a long-term study of *Braya* population dynamics, selecting three populations in locations that span a gradient from minimal to substantial human disturbance. First-year objectives were to determine if significant variation among and within populations existed for (a) numbers of plants in three size classes and (b) size characteristics of plants. Additional objectives were to determine if vegetation and substrate characteristics at one of the locations differed between (c) microsites containing *Braya* and those that did not, and (d) microsites containing *Braya* on and off an old vehicle track.

METHODS

Three populations were chosen for study (Fig. 1, Table 1). Both the Mt. Bross and West Hoosier sites have experienced great historical mining activity and are dissected by old roads and prospects. Mt. Bross is particularly important because it has the largest known population, with an estimated 1,160 individuals (Johnston 1984). The West Hoosier site is significant because it has the second largest population (approximately 430 individuals). Part of the West Hoosier site is owned and managed as a preserve by The Nature Conservancy. The Spout Lake population, the only

TABLE 1. General location descriptions for three *Braya humilis* var. *humilis* populations in central Colorado.

	Location		
Descriptor	Mt. Bross	West Hoosier	Spout Lake
County	Park	Park/Summit	Chaffee
Latitude/longitude	39°19′N,106°06′E	39°22′N,106°05′E	38°47′N,106°25′E
Mountain range	Mosquito	Ten Mile	Collegiate
Elevation (m)	3758	3695	3750
Aspect	East-southeast	East-southeast	North
Slope (degrees)	0–30	20–30	30–40
Human disturbance	High	High-low	Low
Dominant vascular plant species	*Poa rupicola,* *Draba aurea,* *Arenaria obtusiloba*	*Dryas octopetala,* *Carex rupestris,* *Kobresia myosuroides*	*Dryas octopetala,* *Carex rupestris,* *Kobresia myosuroides*

record from the Collegiate Range, consists of approximately 210 individuals and has the largest known population on a site with no evident human disturbance.

Monitoring

Thirty-two permanent, 1-m^2 plots were established at the three locations in August 1985 (22 plots at Hoosier, 4 plots at Mt. Bross, and 6 plots at Spout Lake). Alternate corners of the plots were marked with iron spikes 25 cm long. An iron nail was driven into the ground adjacent to each *Braya* plant; an aluminum tag was attached to each nail. Plant coordinates within the plots were recorded on data forms to facilitate relocation of individual plants in future years. Measurements of rosette diameter and height and counts of numbers of stems, leaves, flowers and fruits were recorded for all *Braya* individuals within the plots. Sampling methodology was adapted from that used by D. W. Inouye and M. B. Cruzan (personal communication) in central Colorado and was conducted during 10 to 15 August 1985.

Plants were separated into three size classes based on their development; ages could not be determined. Seedlings were defined as nonreproductive plants with five or fewer leaves. Juveniles were plants with more than five leaves but without current year's flowers or fruits. Reproductive individuals had current year's flowers or fruits present.

G-tests were used to test for significant association between numbers of *Braya* plants in the three size classes and location. Plant size data were tested for normality using an algorithm in Minitab (Ryan et al. 1982) and were normalized using logarithmic transformation where appropriate. Data were subjected to analysis of variance (ANOVA) to determine if plant size characteristics differed significantly among locations. T-tests were used to assess statistical significance of differences in plant size characteristics on and off the old vehicle tract (termed the cutoff road) within the West Hoosier population.

Vegetation and Substrate Sampling

Total cover of vascular plant species, cover by species, and cover of substrate components (rock, bare ground, and litter) were estimated to the nearest percent for 22 permanent 1-m^2 plots containing *Braya* and 22 randomly placed 1-m^2 plots that did not contain *Braya* at the West Hoosier location. Similar data were collected for plots containing *Braya* on and off the cutoff road. Data were tested for normality as outlined above, transformed as needed, and analyzed using ANOVA. T-tests were used to assess significance of differences in total vegetal cover, cover of dominant vascular plant species, and substrate cover between plots (a) containing or not containing *Braya* and (b) on or off the cutoff road.

RESULTS

Size Structure of Populations

Size structure of *Braya* populations differed among the three locations with a highly significant association between the number of plants in each size class and location (Table 2). Mt. Bross had the largest proportion of seedlings, whereas West Hoosier had the lowest. West Hoosier had the highest proportion of reproductive individuals. Spout Lake had the same proportion of juveniles as did West

TABLE 2. Number (and percentage) of *Braya* plants in three size classes at three locations in central Colorado. Reproductive class includes individuals with current year's flowers or fruits. Juvenile and seedling classes include individuals possessing no current year's reproductive material and that have >5 leaves or 1–5 leaves per plant, respectively.

	Location		
Plant size class	Mt. Bross	West Hoosier	Spout Lake
Reproductive	95 (29%)	139 (47%)	24 (18%)
Juvenile	72 (22%)	139 (47%)	63 (47%)
Seedling	164 (49%)	19 (6%)	47 (35%)
Total	331	297	134

There is a highly significant association ($P<0.005$) between plant class and location (G-test, Sokal and Rohlf 1981).

TABLE 3. Measures of *Braya* plant size and reproductive output in three size classes at three locations in central Colorado. Means ±1 SEM. For definitions of plant classes, see Table 2. Different letters in parentheses within each row denote significantly different means ($P<.05$, least significant difference test, Zar 1974).

	Location			
Plant size class	Mt. Bross	West Hoosier	Spout Lake	P-value
REPRODUCTIVE				
Height (mm)	34.8 ± 1.5(a)	30.2 ± 1.2(b)	20.7 ± 1.6(c)	<0.001
# of stems/plant	4.4 ± 0.5(a)	2.7 ± 0.2(b)	1.4 ± 0.5(c)	<0.001
# of fruits/plant	22.9 ± 0.2(a)	12.1 ± 1.4(b)	6.7 ± 1.2(c)	<0.001
# of leaves/plant	28.1 ± 1.4(a)	23.6 ± 1.0(b)	16.8 ± 1.5(c)	<0.001
Rosette diameter (mm)	27.4 ± 1.0(a)	21.4 ± 0.8(b)	20.4 ± 1.1(b)	<0.001
JUVENILE				
# of leaves/plant	9.9 ± 0.7(a)	12.7 ± 0.6(b)	13.1 ± 0.8(b)	<0.001
Rosette diameter (mm)	12.8 ± 0.7(a)	10.8 ± 0.4(b)	13.4 ± 0.6(a)	<0.006
SEEDLING				
# of leaves/plant	4.1 ± 0.1(a)	4.9 ± 0.1(b)	3.5 ± 0.1 (c)	<0.001
Rosette diameter (mm)	5.5 ± 0.2	5.9 ± 0.6	6.2 ± 0.4	0.178

Hoosier, but it had a much higher proportion of seedlings.

The height, number of stems, fruits, and leaves per plant and rosette diameter of reproductive individuals were significantly different among the three locations (Table 3). Reproductive plants at Mt. Bross were consistently the largest and produced the most reproductive material. Spout Lake consistently had the smallest reproductive individuals; they also produced the smallest amount of reproductive material.

The number of leaves per plant and rosette diameter of juvenile individuals were significantly different among the three locations (Table 3). The Spout Lake juvenile plants were the largest. There were significant differences in the number of leaves per seedling among sites, but not in rosette diameter.

The proportions of plants in the three size classes were significantly different on and off the cutoff road at West Hoosier (Table 4). The plants on the road were mostly reproductive, whereas the plants off the road were mostly juveniles. Although the proportion of seedlings on the road was twice that off the road, seedlings were scarce in both areas. The number of leaves per plant and the diameter of reproductive individuals, as well as the rosette diameter of juveniles, were significantly greater on the road (Table 5).

Vegetal and Substrate Cover

Total vascular plant cover and cover of *Dryas octopetala*, *Carex rupestris*, and *Kobresia myosuroides* were significantly lower on the cutoff road at West Hoosier (Table 6). Plots on the road had significantly greater cover of rock but significantly less litter cover than plots off the road. There was little evidence of disturbance off the road.

Plots containing *Braya* had significantly less total vascular plant cover and cover of *Dryas octopetala*, *Kobresia myosuroides*, and *Polygonum viviparum* than plots lacking *Braya* (Table 7). The rank order of the three plant species with the greatest cover was different in *Braya* plots compared to plots lack-

TABLE 4. Number (and percentage) of *Braya* plants in three size classes on and off the cutoff road at the West Hoosier location in central Colorado. For definitions of plant classes, see Table 2.

	Location	
Plant size class	On cutoff road	Off cutoff road
Reproductive	61 (59%)	78 (40%)
Juvenile	39 (37%)	100 (52%)
Seedling	4 (4%)	15 (8%)
Total	104	193

There is a highly significant association ($P<0.005$) between plant class and location (G-test, Sokal and Rohlf 1981).

ing the plant. The substrate of *Braya* plots was characterized by significantly greater rock and bare ground but lower litter cover.

DISCUSSION

Size Structure and Populations

The different proportions of reproductive, juvenile, and seedling individuals that were observed at the three locations could arise from differences in recruitment, survival, or growth of *Braya* plants. Recruitment of seedlings in harsh environments such as the alpine is probably episodic for many plant species (Billings 1974, Jolls 1982). Factors affecting recruitment could vary substantially over distances on the order of several kilometers. Thus, *Braya* seedling recruitment at the three sites could vary widely among and within years. The small size and large numbers of seedlings at Mt. Bross may indicate more recent establishment at this location, with the few seedlings at West Hoosier resulting from lack of recent recruitment.

Survival of plants within all size classes could also vary greatly among locations and years. The combined effects of differential recruitment and survival could perhaps account for the large observed differences in proportions of size classes at the three locations.

The variation in plant size structure among populations could arise from differential plant growth rates, caused by site quality differences such as soil fertility, soil moisture, length of the growing season, or competition from other species. Difference in rosette diameter may be a phenotypic response to these varying site conditions.

Very little is known about recruitment, survival, and growth of *Braya* individuals. Thus, it is unknown how rapidly the present class structure could change, implications of which are important for the conservation of the taxon. For example, the West Hoosier population consists of reproductive and juvenile individuals with very few seedlings. This population might be senescent with poor prospects for long-term survival. Alternatively, the present dearth of seedlings could simply reflect several recent years of poor seedling establishment, with former seedlings moving into the juvenile and reproductive classes. We presently lack the information necessary to make rational management prescriptions for *Braya*.

Subpopulations only a few meters apart also had different size structures. The lower proportions of juvenile and seedling individuals on the cutoff road may have resulted from increased mortality in the smaller size classes caused by soil erosion on the road. Reproductive individuals, which were nearly always larger than juveniles or seedlings, may have survived better because of their more extensive root systems.

Harris (1985) has reported that *Braya* is octoploid ($2n=56$). Polyploidy may be an important factor in *Braya's* success on old roads. Polyploids are more likely to become adapted to environments disturbed by human activity than are their related diploids (Clegg and Brown 1983). Polyploidy helps to buffer against inbreeding depression and may enhance wide environmental tolerance. Autogamy and polyploidy may help maintain the extremely isolated populations in Colorado (Harris 1985).

Substrate and Plant Associates

Braya microsites at West Hoosier are rocky with much bare ground, minimal litter, and sparse vegetal cover. Typical substrate consists of about 50% rock fragments 1–3 cm in length and about 50% bare ground. Our observations of substrates at other *Braya* locations were consistent with these findings. The low total vegetal cover on the cutoff road is consistent with the findings of Greller (1974), who found total plant cover on 40- to 50-year-old roadcut slopes in the alpine tundra of Rocky Mountain National Park to be less than half of the surrounding natural sites.

Past and Present Disturbance

Braya appears to be a pioneer species of

TABLE 5. Measures of *Braya* plant size and reproductive output in plots on and off the cutoff road at West Hoosier. Means ± 1SEM. For definitions of plant classes, see Table 2.

	Location		
Plant size class	On cutoff road	Off cutoff road	P-value
REPRODUCTIVE			
Height (mm)	30.3 ± 1.9	30.2 ± 1.5	0.96
Number of stems/plant	3.0 ± 0.4	2.4 ± 0.3	0.17
Number of fruits/plant	13.9 ± 2.3	10.7 ± 1.6	0.24
Number of leaves/plant	26.9 ± 1.7	21.1 ± 1.0	0.003
Rosette diameter (mm)	24.2 ± 1.3	18.8 ± 0.7	0.000
JUVENILE			
Number of leaves/plant	13.6 ± 1.3	12.3 ± 0.7	0.35
Rosette diameter (mm)	13.2 ± 0.9	10.0 ± 0.5	0.001
SEEDLING			
Number of leaves/plant	4.8 ± 0.2	5.0 ± 1.7	0.49
Rosette diameter (mm)	7.2 ± 0.2	5.5 ± 0.7	0.23

TABLE 6. Cover of dominant (>1% cover) vascular plant species and substrate components in *Braya* plots on and off of the cutoff road and plots off the cutoff road not containing *Braya* at West Hoosier. Means (%) ± 1 SEM.

	Location			
	Braya plots on road	*Braya* plots off road	Plots without *Braya*	P-value
PLANT SPECIES				
Dryas octopetala	0.1 ± 0.0	12.3 ± 3.9	30.5 ± 5.7	0.001
Carex rupestris	0.8 ± 0.3	6.5 ± 2.3	2.8 ± 1.0	0.060
Kobresia myosuriodes	0.9 ± 0.4	5.8 ± 2.3	10.8 ± 2.5	0.030
Erigeron pinnatisectus	2.0 ± 0.6	1.8 ± 0.6	2.8 ± 0.8	0.056
Polygonum viviparum	1.3 ± 0.3	2.2 ± 0.5	4.5 ± 0.8	0.556
Hymenoxys acaulis	absent	2.2 ± 0.6	1.7 ± 0.6	—
Calamagrostis purpurascens	1.0 ± 0.6	1.8 ± 0.5	2.4 ± 0.8	0.483
Silene acaulis	absent	1.8 ± 1.5	1.3 ± 0.9	—
Total vascular plants	9.8 ± 1.2	39.8 ± 5.3	70.7 ± 5.7	0.000
SUBSTRATE COMPONENTS				
Rock	58.1 ± 5.5	25.1 ± 5.3	16.4 ± 3.2	0.000
Bare ground	35.0 ± 4.9	46.5 ± 4.9	22.5 ± 4.2	0.002
Litter	2.0 ± 0.5	7.5 ± 1.2	17.4 ± 2.2	0.000

TABLE 7. Cover of dominant (>1% cover) vascular plant species and substrate components in plots with and without *Braya* at West Hoosier. Means (%) ± 1 SEM.

	Location		
	Plots with *Braya*	Plots without *Braya*	P-value
PLANT SPECIES			
Dryas octopetala	7.3 ± 2.6	30.5 ± 5.7	0.001
Carex rupestris	4.2 ± 1.4	2.8 ± 1.0	0.45
Kobresia myosuroides	3.8 ± 1.5	10.8 ± 2.5	0.02
Erigeron pinnatisectus	1.9 ± 0.4	2.8 ± 0.8	0.29
Polygonum viviparum	1.8 ± 0.4	4.5 ± 0.8	0.005
Hymenoxys acaulis	1.3 ± 0.4	1.7 ± 0.6	0.58
Calamagrostis purpurascens	1.4 ± 0.5	2.4 ± 0.8	0.29
Silene acaulis	1.0 ± 0.9	1.3 ± 0.9	0.86
Total vascular plants	27.5 ± 4.5	70.7 ± 5.7	0.000
SUBSTRATE COMPONENTS			
Rock	37.6 ± 5.2	16.4 ± 3.2	0.0015
Bare ground	42.1 ± 3.7	22.5 ± 4.2	0.0011
Litter	5.4 ± 1.0	17.4 ± 2.2	0.0000

disturbed areas. In some populations, only a few individuals have been found off these disturbances (E. E. Neely, personal observation). Congeners grow on unstable substrates, such as scree slopes, gravel bars, shorelines, and solifluction lobes (Harris 1985). Many rare taxa in the western flora of North America and their common relatives colonize disturbed habitats (Stebbins 1980). *Braya* may inhabit unstable or disturbed areas because of an inability to compete with other species, as suggested by Griggs (1940) for other species of rare plants.

Of the three populations, Mt. Bross plants appear to be the most vigorous, perhaps because past disturbance has reduced the density or size of other plants, leaving more resources available to *Braya*. The largest plants and those with the greatest amout of reproductive output at Mt. Bross occur mostly on the margins of a rough vehicle path and on spoil banks adjacent to a ditch. The path is level, and the surface is apparently stable. At West Hoosier, the cutoff road is considerably more disturbed than the adjacent areas. Possibly the degree of disturbance on the road is greater than optimum for *Braya*, given the virtual absence of seedlings and small proportion of juveniles.

Observations of *Braya* in the Spout Lake population reinforce the importance of soil disturbance. Here it typically grows in small gravels, scree slopes, and solifluction lobes that have been demonstrated in Rocky Mountain National Park, Colorado, to move downhill at a rate of 3–4 cm year^{-1} (Benedict 1970). *Braya* appears to be preadapted to unstable substrates, making it most successful where there has been some moderate level of natural or man-made disturbance.

The sizes of *Braya* populations before human intervention began is unknown, but if populations at relatively undisturbed sites such as Spout Lake are any indication, populations must have been small. In some cases human disturbance may simulate natural processes that create suitable habitat; however, drastic disturbances such as mine-related activities could greatly reduce or eliminate populations. Because *Braya* is found on calcareous soils derived from rocks such as limestone, which are often highly mineralized, it may be threatened by potential mining activities.

ACKNOWLEDGMENTS

This research was conducted while the senior author was supported by the Colorado Field Office and the Rocky Mountain Heritage Task Force of the The Nature Conservancy, the U.S. Fish and Wildlife Service, and the Colorado Native Plant Society. The authors thank J. G. Harris, M. K. Owens, J. S. Peterson, and L. M. Shultz for critically reading the manuscript and TNC Stewardship Committee, Colorado Chapter, volunteers for assistance with data collection. C. M. Warner drafted the figure.

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BIOGEOGRAPHIC ASPECTS OF LEECHES, MOLLUSKS, AND AMPHIBIANS IN THE INTERMOUNTAIN REGION

Peter Hovingh[1]

ABSTRACT.—Some biogeographical and paleobiological aspects of leeches, mollusks, and amphibians in the Intermountain Region are reviewed. Areas of eastern Nevada and western Bonneville Basin as well as the tristate region of Nevada, Utah, and Idaho are poorly inventoried with respect to many aquatic-dependent animals. Observations of *Batracobdella picta* in the Wasatch Mountains and *Erpobdella punctata* in Tule Valley in the Bonneville Basin extends the western ranges of these leeches in the Great Basin. Life history and size of leeches varies among the study sites in the northern hemisphere. Aquatic mollusk species have diminished greatly in both prehistoric and historic times, as demonstrated by Utah Lake where some 30 species once lived. Eight genera survived into historic times, and perhaps only one species presently lives there. Extinction of numerous mollusks in the Bonneville Basin is still unknown with respect to cause and time. The finding of the Western Spotted Frog (*Rana pretiosa*) in Tule Valley reveals both a different habitat for this species when compared to other study sites and that this species must have occupied the region during Lake Bonneville times. With the exception of the Leopard Frog (*Rana pipiens*), most other amphibians probably migrated into the Bonneville Basin after the desiccation of Lake Bonneville.

For eight years I have examined many ponds and springs to determine the distribution of amphibians and their breeding habitat requirements in such rather diverse arid regions as the Bonneville Basin and the Colorado Plateau as well as the regions of high precipitation, such as the Wasatch and Uinta mountains. It soon became apparent that, with the exception of the threatened and endangered species, very little systematic work had been done on the distribution of native aquatic species in the Intermountain Region. Most of the work was done before 1940. Today, with more and better roads and a very extensive inventory of the water resources, it seemed that new attempts should be made, especially in view of the recent efforts in understanding the hydrological basins and their paleo-history.

This paper reviews certain aspects of leeches, mollusks, and amphibians with the idea that with more information one might better understand their present distribution as well as their past distribution during the era of glaciers and the pluvial lakes. This paper is divided into three separate sections: (1) biogeographical distribution and life history variations of leeches, (2) review of mollusks in the Bonneville Basin, and (3) notes on the distribution of amphibians in Utah and Nevada.

LEECHES

With the exception of Herrmann's work (1970) in Colorado, neither Nevada nor Utah have been methodically investigated for leeches. Twenty-one species were identified from Colorado (Klemm 1982, Herrmann 1970). Ten of these occur in western Colorado in the Middle Rocky Mountain Province and the Colorado Plateau Province (Herrmann 1970). Eight of these western Colorado species were found in Utah (Beck 1954, Barnes and Toole 1981) and four of them were found in Nevada (Klemm 1982). Table 1 lists the distribution. Note the lack of Erpobdellidae in Nevada.

Observations of *Placobdella ornata* (Verrill 1872) in western Colorado, *P. multilineata* (Moore 1953) in the Uinta Basin of Utah, and *P. parasitica* (Say 1824) in Nevada need further clarification. Only in Nevada (Truckee River drainage) does the turtle host exist within this region. *Theromyzon rude* (Baird 1869) was found in both Nevada and Colorado and should be found in Utah. The above leeches will not be discussed further.

Batracobdella picta (Verrill 1872) was reported from Current Creek, Wasatch County, Utah at 1,980 m elevation in a bog (Beck 1954). I found this leech very numerous on larval salamanders of *Ambystoma tigrinum* in

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TABLE 1. Distribution of leeches in the Intermountain Region.

Species	Western Colorado	Utah	Nevada
Glossiphoniidae			
Batracobdella picta (Verrill, 1872)	+	+	
Glossiphonia complanata (Linnaeus, 1758)	+	+	+
Helobdella stagnalis (Linnaeus, 1758)	+	+	+
Placobdella ornata (Verrill, 1872)	+		
Placobdella multilineata (Moore, 1953)		?	
Placobdella parasitica (Say, 1824)			+
Theromyzon rude (Baird, 1859)	+		+
Hirudinidae			
Haemopis marmorata (Say, 1824)	+	+	+
Erpobdellidae			
Dina dubia (Moore and Meyer, 1951)	+	+	
Dina parva (Moore, 1912)	+	+	
Erpobdella punctata (Leidy, 1870)	+	+	
Nephelopsis obscura (Verrill, 1872)	+	+	

Dog Lake (2,660 m elevation, Salt Lake County) and on breeding adults and larval salamanders in Red Pine Lake (2,680 m elevation, Summit County, Weber River drainage) in the Wasatch Mountains. These two observations extend the range of *B. picta* into the Great Basin. This leech was not found in 10 other salamander-inhabited ponds in the Wasatch Mountains (Provo, Weber, and Jordan River drainages) and two ponds of the Uinta Mountains (upper Duchesne River drainage). It was found between 2,062 and 3,224 m elevation in Colorado in 6 lentic water sources (Herrmann, 1970). The scattered distribution of *B. picta* could reflect both the distribution of the amphibian host as well as past mountain glacier distribution.

Glossiphonia complanata (Linnaeus 1758) was found in the bench region of Utah County and at Deer Creek Dam in Wasatch County (Beck 1954). Beck (1954) found *G. complanata* and *Helobdella stagnalis* (Linnaeus 1758) in the "same general distribution of quiet pools of water or slowly moving shallow streams". *Glossiphonia complanata* was found up to 3,610 m elevation in Colorado (Herrmann 1970).

Helobdella stagnalis (Linnaeus 1758) was found in a stream near Laketown (Bear Lake), Utah, the bench region of Utah County, and in Utah Lake (Beck 1954, Tillman and Barnes 1973). In Colorado *H. stagnalis* was found between 1,000 and 3,200 m elevation (Herrmann 1970). I found it feeding on *Nephelopsis obscura* (Verrill 1872) in the mountain ponds of the Uinta Mountains (upper Duchesne River drainage, elevation 3,060 m).

Tillman and Barnes (1973) showed that individual *Helobdella stagnalis* (Linnaeus 1758) produced two broods of young during May and June in Utah Lake. This variation in life history is different from those studied in Canada (Davies and Reynoldson 1976) and the British Isles (Murphy and Learner 1982) (Fig. 1). At these latter locations, the adults died after producing young; in some locations two generations per year occurred and in other locations only one generation per year occurred. Water temperature may be a determinant of the two life history patterns in Canada (Davies and Reynoldson 1976). It is unknown what the determinants of *H. stagnalis* life history in Utah Lake are, or if this life history variation is limited to Utah Lake.

Nephelopsis obscura (Verrill 1872) is perhaps the most common leech in Uinta Mountain ponds and may be the top predator in the ponds that do not contain salamanders. In the Uinta Mountain ponds, I observed *N. obscura* at night with densities of four to six leeches per m^2 of surface water in a pond that was at the most 1 m deep. Daytime observations were common in June and July, with densities less than one leech per m^2 and rare in September. Cocoons were deposited from early June to autumn, with the prevalent deposition occurring during late July. Growth patterns show, in late June, sizes between 0.01 and 0.85 g, with a group between 0.2 and 0.3 g (Fig. 2). During July, the large individuals

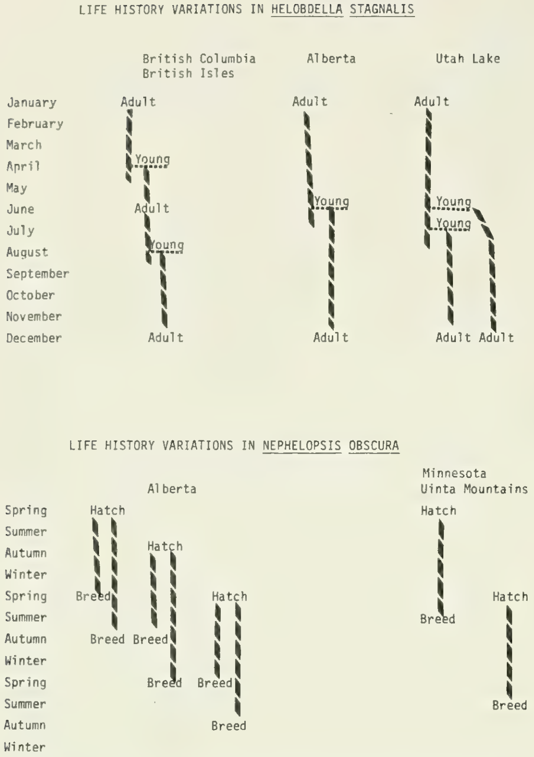
LIFE HISTORY VARIATIONS IN HELOBDELLA STAGNALIS
British Columbia British Isles
Alberta
Utah Lake
January
February
March
April
May
June
July
August
September
October
November
December
Adult
Young
Adult
Young
Adult
Adult
Young
Adult
Adult
Young
Young
Adult Adult
LIFE HISTORY VARIATIONS IN NEPHELOPSIS OBSCURA
Alberta
Minnesota Uinta Mountains
Spring
Summer
Autumn
Winter
Spring
Summer
Autumn
Winter
Spring
Summer
Autumn
Winter
Hatch
Hatch
Breed
Hatch
Breed Breed
Breed Breed
Breed
Hatch
Breed
Hatch
Breed

Fig. 1. Life history patterns of *Helobdella stagnalis* in British Columbia and Alberta (Davies and Reynoldson 1976), British Isles (Murphy and Learner 1982), and Utah Lake, Utah (Tillman and Barnes 1973) (upper figure). Life history patterns of *Nephelopsis obscura* in Alberta (Davies and Everett 1977), Minnesota (Peterson 1983), and the Uinta Mountains, Utah (based on size alone) (lower figure).

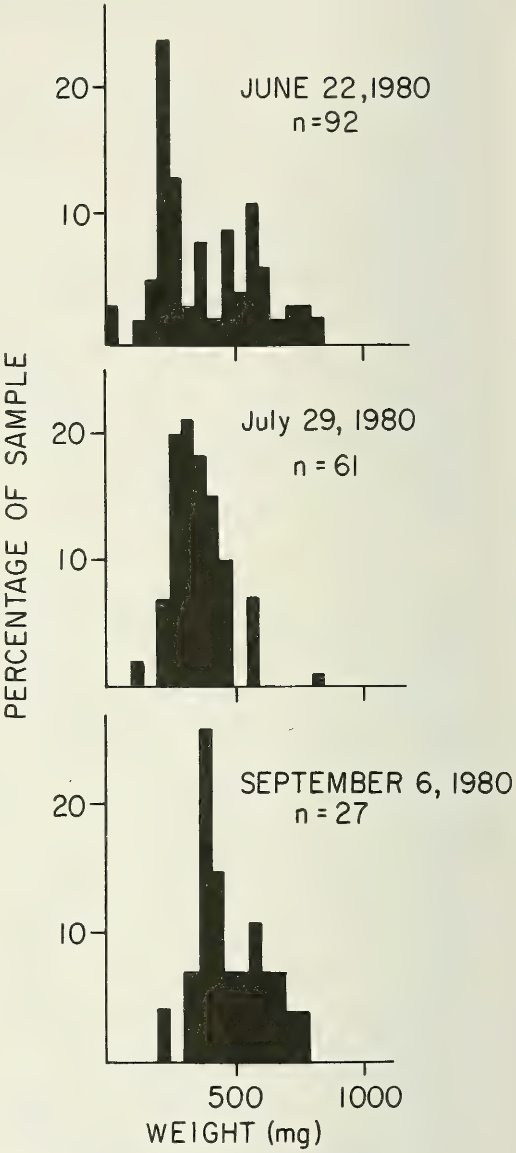

Fig. 2. Weights of *Nephelopsis obscura* in a Uinta Mountain pond during the summer. The leeches were weighed to the nearest 10 mg. For comparison, consult with Davies and Everett (1977) and Peterson (1983).

(larger than 0.5 g) die and can be seen in the bottom of the ponds. Growth continues to September. These data indicate that there is only one generation of young each year. One generation of young each year is similar to populations in Minnesota (Peterson 1983) and contrasts with the two-generation strategy in Alberta (Davies and Everett 1977) (Fig. 1). Sizes of leeches may not be an appropriate indicator of generation (Collins and Hohmstrand 1984a, b). *Nephelopsis obscura* reaches sizes of up to 1.2 g in the Uinta Mountains compared with populations in Alberta (0.41 g) and Minnesota (over 4.0 g) (Davies and Everett 1977, Collins and Hohmstrand 1984). The scarceness of leeches less than 0.1 g in the Uinta Mountain ponds contrasts sharply with the abundance of leeches in this class size in Alberta. It was found in the bench regions of Utah and Salt Lake counties in freely running streams or in shallow ponds (Beck 1954). It has not been recorded in Utah Lake. It was found only in lentic habitats in Colorado between 1,650 and 3,200 m elevation (Herrmann 1970) and only in lotic habitats in Michigan (Klemm 1972). Reynoldson and Davies (1980) noted that *N. obscura* was rather sensitive and intolerant to the changes in osmolarity of the aquatic medium.

Erpobdella punctata (Leidy 1870) was

found in the bench region of Utah County and at 1,740 m on Cove Mountain, Sevier County (Beck 1954). It has been found in Utah Lake (Barnes and Toole 1981). I found it in Red Pine Lake (2,680 m elevation, Weber drainage, Summit County) and in Solitude Lake (2,740 m elevation, Big Cottonwood Creek drainage, Salt Lake County) in the Wasatch Mountains and in five springs-wetlands in Tule (White) Valley (elevation 1,350 m, Millard County). The aquatic systems in Tule Valley have been isolated from other Bonneville Basin aquatic systems for some 13,000 years. In Tule Valley the specific conductance of the inhabited waters varied between 1,200 and 2,500 umhos/cm at 25 C, depending on the location in each wetland as well as the time of the year. Reynoldson and Davies (1980) noted that *E. punctata* was much more tolerant to variations in osmolarity than *Nephelopsis obscura* (Verrill 1872). Such tolerance might explain the presence of *E. punctata* in the interior of the Bonneville Basin, where it may exist as a relict species. Herrmann (1970) found *E. punctata* in both lentic and lotic habitats between 1,044 and 3,232 m elevation in Colorado. The leech was found in waters with pH variations of 6.3 to 10.3 (Herrmann 1970) and as low as pH 5.0 in Michigan (Klemm 1972). Davies et al. (1977) noted variations in life history patterns with *E. punctata* populations in Alberta and that the differences might be explained by interspecific competition with *N. obscura*.

Two other Erpobdellidae, *Dina dubia* (Moore and Meyer 1951) and *D. parva* (Moore 1912), have been reported from Utah. *Dina dubia* was found in association with *Nepholopsis obscura* (Verrill 1872) in lotic habitats in the bench region of Utah County (Beck 1954). *Dina parva* was found in Utah Lake (Barnes and Toole 1982).

Haemopis marmorata (Say 1824) was found in the bench region of Utah County, eastern slope of the Aquarius Plateau in Garfield County, and at Deer Creek Dam in Wasatch County (Beck 1954). It was found to tolerate the greatest total dissolved solids (2,807 mg/l) of all the other leeches and was found between 1,044 and 2,975 m elevation in Colorado (Herrmann 1970).

In the Colorado mountains, Pennak (1968) described the semidrainage lakes. In these lakes certain fauna and flora form a characteristic assemblage. The tiger salamander (*Ambystoma tigrinum*) and the yellow pond lily (*Nuphar polysepalum*) are the characteristic animal and plant. *Glossiphonia complanata*, *Nephelopsis obscura*, and *Helobdella stagnalis* occur together in these lakes (Pennak 1968). Other leeches found in semidrainage lakes include *Batracobdella picta*, *Batracobdella phalera*, *Dina dubia*, *Erpobdella punctata*, *Haemopis marmorata*, *Haemopis kingi*, and *Theromyson rude* (Herrmann 1970). The semidrainage ponds in the Uinta Mountains occur with the tiger salamander, yellow pond lily, *N. obscura*, and *H. stagnalis*. It would be interesting to study these ponds over the entire Uinta Mountains to determine how these ponds relate to the Colorado semidrainage ponds. During the glaciation some 25,000 years ago, all of these ponds and lakes were under ice fields and, thus, the ecology of the Uinta Mountain ponds and lakes may have evolved separately from the Colorado Rocky Mountain ponds and lakes.

MOLLUSKS

Of some 100 species of mollusks in the Great Basin, some 50 species are found along the Highway 89-91 axis from Idaho to Arizona. With only Fish Springs National Wildlife Refuge being extensively inventoried in the western Bonneville Basin, much of the Bonneville Basin and eastern Nevada are still very fertile areas for studying the assemblage of molluscan species.

The desiccation of the pluvial lakes left many "semifossils," a name coined by early collectors who gathered empty shells from arid regions in the Bonneville Basin (Call 1884). Other collectors gathered shells from aquatic regions such as Utah Lake and Bear Lake and noted that they were fresh. In reviewing the literature it is difficult to know what specimens were found living. Many molluscan species require the examination of the soft parts for identification, and soft parts were not collected.

A major problem today is to determine what mollusks were present in the region before Lake Bonneville, the distribution of mollusks with the rising and desiccating waters of Lake Bonneville, and the present distribution of mollusks in the numerous basins of the Bonneville Basin and adjacent basins of Nevada. This information could tell us very much about the evolution of the present-day aquatic flora and fauna of the water sources in the numerous basins.

Both Utah Lake and Bear Lake have an abundant record of mollusks. Some 30 species of mollusks have been identified from Utah Lake environs. The taxa and their references are:

Unionidae: *Anodonta oregonensis* Lea 1838 (Chamberlin and Jones 1929, Jones 1940a), *Anodonta nuttalliana* Lea 1838 (Call 1884, Chamberlin and Jones 1929, Henderson 1931, Jones 1940a), *Anodonta wahlametensis* Lea 1838 (Chamberlin and Jones 1929, Jones 1940a).

Sphaeriidae: *Sphaerium pilsbryanum* Sterki 1909 (Baily and Baily 1951–1952, Call 1884, Chamberlin and Jones 1929, Jones 1940a), *Pisidium compressum* Prime 1851 (Baily and Baily 1951–1952, Call 1884, Chamberlin and Jones 1929, Jones 1940a), *Pisidium casertanum* Poli 1791 (Baily and Baily 1951–1952, Jones 1940a). *Pisidium variabile* Prime 1851 (Jones 1940a).

Valvatidae: *Valvata humeralis* Say 1829 (Baily and Baily 1951–1952, Chamberlin and Jones 1929), *Valvata utahensis* Call 1884 (Baily and Baily 1951–1952, Bickel 1977, Call 1884, Chamberlin and Jones 1929, Taylor 1966, Jones 1940a).

Hydrobiidae: *Fluminicola fusca* Haldeman 1847 (Baily and Baily 1951–1952, Call 1884, Chamberlin and Jones 1929, Jones 1940a), *Fluminicola seminalis* Hinds 1842 (Jones 1940a), *Amnicola limosa* Say 1817 (Baily and Baily 1951–1952, Chamberlin and Jones 1929, Henderson 1931, Jones 1940a), *Fontelicella (Paludestrina) longinqua* Gould 1855 (Jones 1940a), and *Tyonia (Paludestrina) protea* Gould 1855 (Jones 1940a).

Lymnaeidae: *Lymnaea stagnalis* Say 1821 (Call 1884, Chamberlin and Jones 1929), *Lymneus elodes* Say 1821 (Baily and Baily 1951–1952, Chamberlin and Jones 1929), *Fossaria modicella* Say 1825 (Chamberlin and Jones 1929, Jones 1940a), *Fossaria obrussa* Say 1825 (Chamberlin and Jones 1929, Jones 1940a), *Fossaria parva* Lea 1841 (Baily and Baily 1951–1952), *Stagnicola utahensis* Call 1884 (Baily and Baily 1951–1952, Bickel 1977, Chamberlin 1933, Chamberlin and Jones 1929, Jones 1940a), *Stagnicola caperata* Say 1929 (Baily and Baily 1951–1952), *Stagnicola proxima* Lea 1856 (Baily and Baily 1951–1952), and *Stagnicola hemphilla* Baker 1934 (Baily and Baily 1951–1952).

Physidae: *Physella propinqua triticea* Lea 1856 (Baily and Baily 1951–1952), *Physella utahensis* Clench 1925 (Baily and Baily 1951–1952, Barnes and Toole 1981, Bickel 1977, Chamberlin and Jones 1929, Jones 1940a).

Planorbidae: *Gyraulus similaris* Baker 1917 (Baily and Baily 1951–1952), *Gyraulus vermicularis* Gould 1847 (Chamberlin and Jones 1929, Jones 1940a), *Helisoma (Carinifex) newberryi* Lea 1858 (Baily and Baily 1951–1952, Call 1884, Chamberlin and Jones 1929, Taylor 1966, Jones 1940a), *Promenetus (Menetus) exacuous* Say 1821 (Baily and Baily 1951–1952, Chamberlin and Jones 1929), and *Planorbella (Helisoma) trivolvis* Say 1817 (Chamberlin and Jones 1929, Jones 1940a).

Ancylidae: *Ferrissia fragilis* Tryon 1863 (Baily and Baily 1951–1952), and *Ferrissia rivularis* Say 1817 (Chamberlin and Jones 1929).

Of these mollusks in Utah Lake only *Anodonta* (Henderson 1931), *Pisidium compressum* (Call 1884), *Physella propinqua triticea* (Baily and Baily 1951–1952), *Physella utahensis* (Barnes and Toole 1981, Bickel 1977), *Helisoma newberryi* (Center for Health and Environmental Studies 1975, Call 1884), *Fluminicola fusca* (Call 1884), *Valvata utahensis* (Call 1884), *Lymnaea stagnalis* (Call 1884), and *Stagnicola utahensis* (Chamberlin 1933) have been found living in Utah Lake. Presently *Physella utahensis* may be the only living species in Utah Lake (Barnes and Toole 1981).

The extinction of mollusks at Utah Lake and Bear Lake raises some questions. Was there a general extinction of mollusks in the Great Basin lakes during some specific period, or did each species become extinct with species specific causes and with lake specific causes? Did the rising waters of the prehistoric pluvial lakes cause any extinction of mollusks in the lakes and isolated springs, or did the rising waters distribute the isolated mollusks throughout the basin? Has there been any postpluvial evolution of mollusks?

The Bear Lake molluscan assemblage showed that *Helisoma newberryi* (the most common gastropod) was radiodated at 8270 B.P. (from 1.2 m deep at the Willis Ranch terrace, elevation 1,814 m), 7700 B.P. (0.3 m deep at the Lifton bar shoreline, elevation, 1,808 m), and 7880 B.P. (less than 1 m above Bear Lake shoreline, 1,806 m elevation) (Williams et al. 1962). These dates indicate that *H. newberryi* became extinct at a rather specific time and perhaps its extinction was related to the lowering of Bear Lake (Williams et al. 1962). A second report listed the age of *H. newberryi* and *Sphaerium* sp. at the Bear Lake shoreline at 12,000 B.P. (Smart 1963). This would suggest that the extinction of mollusks at Bear Lake included an assemblage of species. Unfortunately, the dates are in conflict (fictitious results can result under several circumstances, see Keith and Anderson 1963, Riggs 1984, Rubin and Taylor 1963). It would be important to reexamine the ages of mollusks of Bear Lake and to examine the ages of mollusks at Utah Lake and other lakes in the Great Basin.

Whereas many molluscan species have limited present-day distribution, some of these species may have a widespread fossil distribution. *Stagnicola pilsbryi* Hemphill, 1890, is an exception, with its distribution being limited to Fish Springs National Wildlife Refuge and having no fossil record (Russell 1971, Taylor et al. 1963). Presently *S. pilsbryi* is considered extinct. It is unknown if *S. pilsbryi* evolved at Fish Springs after the desiccation of Lake Bonneville (Russell 1971).

More studies of molluscan biogeographic distribution and habitat requirements in the Intermountain Region are needed to understand the evolution of the aquatic systems in the Great Basin (Yen 1951, Taylor et al. 1963, Taylor 1960, Russell 1971, Murray 1970).

AMPHIBIANS

Fourteen species of amphibians occur in Nevada and in Utah, with 12 species common to both states (Linsdale 1940, Banta 1965, La Rivers 1942, Tanner 1931). Most of these amphibians can be placed into one of two groups. The first group is postulated as arriving into the Intermountain Region from the south and is largely confined to the Colorado River drainage in Utah and Nevada (Tanner 1978). These species include *Bufo cognatus*, *B. microscaphus*, *B. punctatus*, *B. woodhousei*, *Hyla arenicolor*, *Rana onca*, and *R. fisheri*. *R. onca* and *R. fisheri* may be part of the *Rana pipiens* "complex."

Bufo woodhousei is the only amphibian arriving from the south that penetrates into the Bonnevillle Basin and extends along the axis of Interstate 15 to and including portions of the Snake River drainage of Idaho. In the Bonneville Basin, *B. woodhousei* is found in the Sevier River drainage and in the isolated Snake Valley Basin in western Utah (Tanner 1931). Another species, *Scaphiopus intermontanus* also came from the south because there was not much suitable habitat during the pluvial times for this amphibian to breed (Hovingh et al. 1985). *Scaphiopus intermontanus* is not dependent upon water for migration as is the other species in the first group.

The second group is postulated as arriving from the north, from the east, or from the west. This second group includes *Ambystoma tigrinum*, *Hyla regilla*, *Pseudacris triseriata*, *Bufo boreas*, *Rana pretiosa*, and *R. pipiens*. If one were to ask if any amphibians occurred in the Intermountain Region during the pluvial and glacial era some 25,000 years ago, this second group would have the most likely candidates. The Leopard Frog (*R. pipiens*), being found in many isolated springs throughout the Bonneville Basin and in numerous basins of Nevada, in mountainous habitat, and adapting to flood plains of the White River (Uintah County), is one species that most likely occupied the region during the pluvial times.

The Western Toad (*Bufo boreas*) largely inhabits the northwest United States and occupies areas in northern Nevada and the mountain regions of Utah. There are some recognized subspecies in central and southern Nevada (Linsdale 1940). The Western Toad has not been found along the Utah-Nevada border (in particular, the Snake and Spring valleys). This toad breeds in the valley floors in Nevada and up to 3,050 m elevation in the mountains of Utah. When the species breeds in the valley floors of Utah, there may be some site competition with *B. woodhousei*. It seems that if the Western Toad occupied the Bonneville Basin during the pluvial times, it would presently occupy the valleys of the Utah-Nevada border.

The Tiger Salamander (*Ambystoma tigrinum*) and the Chorus Frog (*Pseudacris triseriata*) are very common in the aquatic systems of the Uinta Mountains in regions that formerly were occupied by glaciers. The Tiger Salamander is also common in the ponds and reservoirs along the Wasatch Front and in the Wasatch Mountain lakes (Tanner 1931). The Chorus Frog is less abundant along the lower elevations of the Wasatch Front (Tanner 1931) and is scarce in the high mountain lakes of the Central Wasatch Mountains. Neither species has been collected in Nevada, although the salamander is found in both the Raft River and Pine Valley mountains. It would seem that if the Tiger Salamander and Chorus Frog were present during Lake Bonneville times, their distribution would occur in regions of eastern Nevada and western Bonneville Basin (Spring and Snake valleys). Their limited distribution might be explained by (1) relict populations during the pluvial times with no opportunity for extending their range into the Bonneville Basin, or (2) migration into Utah in postpluvial and postglacial times along the Uinta Mountains and fanning out via the Wasatch Mountains to the Pine Valley Mountains in the south and the Raft River Mountains in the north. In the cases of the Tiger Salamander and the Chorus Frog (two eastern amphibians), one could postulate that between Lake Bonneville and the alpine glaciers there was not any habitat for these amphibians.

The Pacific Treefrog (*Hyla regilla*) is common in California and Oregon and in isolated populations in both the Colorado River drainage of Nevada and southwestern Utah, in central Nevada, and in the Raft River Mountains of Utah (Tanner 1931, Reynolds and Stephens 1984). This particular frog may have extended its range eastward during the pluvial times and now in the postpluvial era remains in isolated pockets.

The Western Spotted Frog (*Rana pretiosa*) occurs in many relict populations from near Juneau, Alaska, southward throughout Washington, Oregon, British Columbia, Idaho, western Montana, the upper Humboldt River drainage in Nevada, Yellowstone National Park, and the Big Horn Mountains in Wyoming and in isolated pockets of the Bonneville Basin and drainage system in Utah (Dunlap 1977, Turner and Dumas 1972, Morris and Tanner 1967, Tanner 1931). The museum records of the University of California (Berkeley), Brigham Young University (Provo), University of Utah (Salt Lake City), and the University of Michigan (Ann Arbor) show the distribution in Utah to include the Snake Valley and Deep Creek drainage in the western Bonneville Basin and the Mono Lake (Juab County), the San Pitch River (a tributary of the Sevier River), and numerous locations in Salt Lake, Utah, Summit, and Wasatch counties in the eastern Bonneville Basin. Western Spotted Frogs have not been found in the drainage of Thousand Springs Creek in northeastern Nevada and northwestern Utah, in the Raft River Mountain region, and in the main Sevier River drainage. Thus, from the records, the distribution of the Western Spotted Frog in the Bonneville Basin is several isolated populations.

In 1980 I found the Western Spotted Frog in Tule (White) Valley in Millard County, Utah. Tule Valley lies between Snake Valley on the west and the Sevier drainage basin on the east. Tule Valley has been isolated from the Lake Bonneville aquatic system for 14,000 years, and highly aquatic species such as the Western Spotted Frog could only occur in Tule Valley if it also occurred in the Lake Bonneville environs (assuming no human intervention). Thus, one may assume that the Western Spotted Frog along with the Leopard Frog occupied the Bonneville Basin at the time of Lake Bonneville.

In examining the Tule Valley populations, one finds the Western Spotted Frog has adapted to a more saline environment than that found in other parts of its distribution. The wetlands lie between 1,347 and 1,350 m elevation on the valley floor, and most have warm water sources (25-19 C). The total dissolved solids varies in the springs from 1,000 to 1,400 mg/l (Stephens 1977) and the specific conductance varies between 1,000 and 3,000 umhos/cm at 25 C, depending on the location in the wetlands and the time of year. In Tule Valley, the Western Spotted Frog breeds in the cold water portion (the most distal from the spring source) of the warm water springs.

Although amphibians are considered terrestrial animals, the arid regions often limit populations from extending their ranges. The distribution of these amphibians may be very local, endemic, and relict as are the Tule Valley populations of the Western Spotted Frogs. The distribution of amphibians in the Intermountain Region can readily be the result of the pluvial and glacial eras and the subsequent desiccation. However, one must presently be careful in noting the presence or absence of relict populations. These populations may be a result of disturbances by natural predators or humans and human-associated animals. For instance, the Tiger Salamander replaced a viable breeding population of Leopard Frogs in an Emigration Canyon spring (Salt Lake County) over a period of 20 years (1963-1983). Leopard Frogs are known to eliminate Western Spotted Frogs (Dumas 1966). Spadefoot Toad (*Scaphiopus*) tadpoles are thought to eliminate other amphibian tadpoles (Creusere and Whitford 1976). Introduced bass, sunfish, and bullfrogs are highly destructive of native amphibian populations (Turner 1962, Licht 1974). Human utilization of scarce desert waters for agriculture and domestic uses deprives the amphibians of necessary breeding habitat (Turner 1962, Morris and Tanner 1969). It should be noted that many amphibian populations along the Wasatch Front in Utah and Salt Lake counties no longer exist; even though the breeding habitat still remains, it is surrounded by housing developments or is adjacent to new highways.

Certainly more fieldwork is needed in the biogeography of amphibians in the Intermountain Region. Particular attention must be applied to the Utah-Nevada border, the Raft River Mountains and Thousand Spring Creek, Goose Creek, and other drainages of the Snake River in the tristate region of Idaho, Utah, and Nevada. Breeding habitats must be identified and characterized.

ACKNOWLEDGMENTS

I would like to thank Dr. Donald J. Klemm (U.S. Environmental Protection Agency, Environmental Monitoring and Support Laboratory, Cincinnati, Ohio 45268) for the identification of *B. picta, H. stagnalis, N. obscura* and *E. punctata*. Without his cooperation the review of the leeches would not have been written.

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HATCHING CHRONOLOGY OF BLUE GROUSE IN NORTHEASTERN OREGON

John A. Crawford[1], Walter Van Dyke[2], Victor Coggins[3], and Martin St. Louis[3]

ABSTRACT.—Hatching chronology of Blue Grouse (*Dendragapus obscurus*) in northeastern Oregon was determined from 431 immatures examined from 1981 to 1985. Young hatched from 1 May through 8 July; median hatching dates for the five years ranged from 27 May to 5 June. Peak hatching in Oregon occurred from one to four weeks earlier than in most portions of the range of Blue Grouse but were similar to north central Washington and Idaho. Variations in hatching dates possibly were related to rainfall.

Information concerning hatching chronology is essential for study of the breeding ecology (e.g., survival and recruitment) of bird populations and is useful for determining optimum times for population censusing. Bendell and Zwickel (1985) summarized hatching times of Blue Grouse from 25 locations throughout the range and noted that peak hatching dates, which ranged from 24 May to 11 July, were earliest near the center of distribution. Results of research on Vancouver Island, British Columbia (Bendell 1955, Zwickel and Bendell 1967, King 1971, Redfield 1975), southwestern Alberta (Boag 1965), and southcentral Montana (Mussehl 1960) indicated that peak hatching times of Blue Grouse were remarkably similar, mid- to late June, among these diverse locations.

In contrast, Blue Grouse were reported to hatch from two to four weeks earlier in north-central Washington (Standing 1960, Henderson 1960, Bauer 1962, Zwickel 1973) and western Idaho (Caswell 1954). Brown and Smith (1980) noted that most immatures were from six to eight weeks old at the end of August (indicating most hatched from early to mid-July) on their study area in eastern Arizona. Redfield (1975) and Zwickel (1977) found hatching dates of Blue Grouse differed among years on Vancouver Island and attributed these differences to annual variations in weather. Data are unavailable regarding hatching times from several portions of the range of this species, including Oregon. The purpose of this project was to determine the hatching chronology of Blue Grouse in northeastern Oregon and to examine, evaluate, and assess annual variations in hatching times.

From 1981 through 1985 wings and tails of 775 Blue Grouse taken by hunters from 29 August to 30 September each year were collected in Wallowa County in northeastern Oregon. Blue Grouse in this region typically occupy coniferous forest, timbered draws, and adjacent grass-shrubland habitats at elevations ranging from 600 to 1,500 m. Age of birds was classified as adult or immature (young of the year) based on the condition of the outer two primaries (Bunnell et al. 1977) and the presence of juvenal feathers in the wing or tail. Sufficient information (date of kill and primary feathers present) was available to estimate hatching dates for 431 of 467 immatures examined. Dates of hatching were based on replacement rate of primary feathers (Zwickel and Lance 1966) and corrected for bias (Redfield and Zwickel 1976).

Only 17 of the 431 immatures had completed molting of the primaries and, in all instances, presence of sheathing material at the base of the eighth primary indicated the molt was recently finished. These birds were assigned the maximum age of 123 days. Median (suggested by Redfield 1975) and mean hatching dates and periods of peak (14-day period in which greatest number of young hatched) and maximum (time interval during which > 70% of young hatched) hatching were based on young hatched/day. These data were summarized by weekly intervals, beginning with the earliest hatching date. One-way analysis of variance and the Student-

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TABLE 1. Percent of young Blue Grouse hatched during weekly intervals and median and range of hatching dates, northeastern Oregon, 1981–1985.

Category	1981 (n = 44)	1982 (n = 34)	1983 (n = 106)	1984 (n = 81)	1985 (n = 164)
WEEK					
1–7 May	2	0	1	0	1
8–14 May	2	3	5	1	6
15–21 May	23	15	8	6	15
22–28 May	16	24	47	21	23
29 May–4 June	27	32	18	19	26
5–11 June	11	21	7	26	13
12–18 June	9	6	7	14	11
19–25 June	5	0	8	7	4
26 June–2 July	5	0	1	3	0
3–9 July	0	0	0	4	2
HATCHING DATES					
Mean	30 May	30 May	30 May	7 June	1 June
Median	29 May	31 May	27 May	5 June	31 May
Range	1 May–29 June	14 May–18 June	5 May–30 June	13 May–8 July	5 May–8 July

TABLE 2. Periods of peak (14-day period when most young hatched) and maximum (time during which > 70% of young hatched) hatching of Blue Grouse.

Location	Dates of peak hatching	Period of maximum hatching: Dates	Period of maximum hatching: % young hatched	Source
Vancouver Island, British Columbia	15–21 June[1] 17–30 June[2]	8–28 June 11 June–1 July	80 72	Bendell 1955, King 1971 Zwickel and Bendell 1967
Hardwicke Island, British Columbia	—	4–25 June	—	Zwickel (personal communication)
Southwestern Alberta	14–21 June	—	—	Boag 1965
North central Washington	22 May–4 June	—	—	Standing 1960, Bauer 1962 Zwickel 1973
	10 May–25 May	—	—	Zwickel (personal communication)
South central Montana	14–21 June	9 June–3 July[3]	80	Mussehl 1960
Western Idaho	25 May–7 June	—	—	Caswell 1954
Northeastern Oregon	20 May–2 June	18 May–7 June	71	This study

[1] Some authors reported peak hatching periods of < 14 days.
[2] Approximate mean dates for three years (two areas/year).
[3] Average dates for two years.

man-Keuls mean separation test (Snedecor and Cochran 1967) were used to test for differences in mean hatching dates among years. Precipitation and mean temperatures for March, April, and May of each year were obtained for the Enterprise weather station (Climatological Data Oregon, NOAA) and compared to median hatching dates.

Hatching dates of Blue Grouse in northeastern Oregon (Table 1) ranged from 1 May (1981) to 8 July (1984 and 1985). Median hatching dates (Table 1) ranged from 27 May (1983) to 5 June (1984). Comparisons of mean hatching dates, all of which were ± 3 days of respective median dates, indicated that hatching in 1984 (7 June) was significantly ($P < 0.05$) later than in the other four years (range 30 May–1 June); no other differences were detected. Length of the hatching period for all years combined, 10 weeks, was identical to that reported by Zwickel and Bendell (1967) for Blue Grouse on Vancouver Island. The mean annual length of the hatching period in northeastern Oregon was 54 days, however. In this study, hatching was concentrated from mid-May to mid-June (Table 1).

For all years combined, 54% of the young hatched in May, 45% in June, and 1% in July. Zwickel and Bendell (1967) noted peak hatching lasted approximately two weeks on Vancouver Island, and the period of maximum hatching (> 70%) took place within three to four weeks; they found that 67% of the young hatched during the peak, 7% before, and 26% after the peak. For northeastern Oregon the peak of hatching (55% of the young) occurred from 20 May to 2 June (Table 2); 9% hatched before the peak and 36% after.

Maximum hatching of young (71%) took place from 18 May to 7 June. Median hatching date for the five years was 31 May and the mean was 1 June. Dates of peak hatching of Blue Grouse in northeastern Oregon (Table 2) were from two to four weeks earlier than those reported for British Columbia, Alberta, Montana, and Arizona (Bendell 1955, Mussehl 1960, Boag 1965, Zwickel and Bendell 1967, Brown and Smith 1980, Zwickel, personal communication) and one week earlier than hatching in northern California and northern Nevada (Zwickel, personal communication). Hatching dates were similar to those reported in north central Washington (Standing 1960, Henderson 1960, Bauer 1962, Zwickel 1973) and Idaho (Caswell) 1954.

Factors affecting the timing of reproductive activities of Blue Grouse throughout their range are incompletely understood. King (1971) found that hatching times were related to elevation; Blue Grouse in subalpine areas hatched approximately 3.5 weeks later than those living at lower elevations. Marshall (1946) proposed that plant phenology in spring influenced the timing of migration of Blue Grouse, which in turn affected breeding times. Plant phenology also may directly influence breeding times (Zwickel, personal communication). Plant phenology throughout the range of Blue Grouse is strongly influenced by elevation and latitude. Blue Grouse populations with which our data were compared (Table 2), except for birds in north central Washington and western Idaho, inhabited areas either farther north by > 4° (British Columbia and Alberta) or at higher elevations (≥ 1800 m in Montana and Arizona), which may account for earlier breeding in northeastern Oregon. The study site in Washington was approximately 3° north of our area but was lower in elevation (450–900 m) and the study area of Caswell (1954) in Idaho bordered northeastern Oregon.

Zwickel (1977) noted that temperature and precipitation partially accounted for annual differences in hatching chronology within populations; earlier hatching coincided with warm, dry conditions during April and May. Redfield (1975) suggested that annual differences within populations were related to spring temperatures. In our study the median hatching date in 1984 was from 6 to 10 days later than in any of the other four years. Comparisons of median hatching dates with mean monthly temperature and total monthly precipitation during March, April, and May reveal that precipitation during April/May (10.7 cm) and from March through May (15.4 cm) 1984 was the highest of the five years; mean values for the other four years were 9.2 cm and 13.4 cm, respectively. Temperature data for 1984 were similar to the other four years. No other trends were apparent from these data, and limited sample size (five years) precluded statistical testing.

We concluded that hatching times of Blue Grouse in northeastern Oregon were similar in most years. Mean hatching date differed only in 1984; all dates were within a 10-day interval. Latest hatching corresponded to the wettest spring of the five years. Hatching dates in northeastern Oregon were consistent with the observation of Bendell and Zwickel (1985) of early breeding within the central portion of the range of Blue Grouse.

ACKNOWLEDGMENTS

We would like to thank T. F. Haensly and S. M. Meyers for their assistance in determining sex and age of birds. The manuscript was reviewed by F. C. Zwickel, E. C. Meslow, and R. L. Jarvis. Special appreciation is expressed to F. C. Zwickel for generously sharing unpublished data. This is Technical Publication 7838 of the Oregon Agricultural Experiment Station.

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NEW SOUTH AMERICAN LEAFHOPPERS IN THE GENUS *DOCALIDIA*, WITH A KEY TO 37 SPECIES (CICADELLIDAE: COELIDIINAE, TERULIINI)

M. W. Nielson[1]

ABSTRACT.—Ten new species of *Docalidia* are described and illustrated. These are *pennyi, gracilitas, zanoli, triquetra, paracrista, convexa, setacea,* and *caterva* from Brazil and *vesica* and *vella* from Peru. A key to males of 37 species described since the last revision of the genus is included. The number of known species is now 116, making *Docalidia* the largest teruliine genus.

Since the treatment of the genus *Docalidia* in a revision of the tribe Teruliini (Nielson 1979), several new species in the genus have been described (Nielson 1982a, 1982b, 1982c). In this paper 10 additional new species are described and illustrated, bringing the total to 116 known species in this the largest of the teruliine genera.

The richness of the fauna of this group in South America (only one species known in Central America and one in the West Indies) is staggering. The number of known species prior to 1979 was 21 and since then the number has increased nearly 600%. Most of the new species described herein and in earlier papers were the result of collections made during the last 20 years. As new areas of tropical America become more accessible and collections more extensive, many new species of *Docalidia* will be found.

Docalidiine leafhoppers are small to medium-sized, robust species with short, broad heads. The crown is short, broad, depressed, but usually not carinate, and the pronotum is noticeably inflated in many species. A very well-developed median clypeal carina distinguishes this group from other similar appearing genera that usually have a weakly developed clypeal carina. The long, usually slender, aedeagus with or without a single subapical ventral spine, simple to ornate style and 10th segment processes, and the broad plate will readily distinguish the group from all other teruliine genera.

A key to males of 37 species not previously keyed is given to accommodate species described here and in my three earlier papers cited above. The remainder are keyed in my 1979 paper.

Hosts and biology of these leafhoppers are poorly known. Paucity of populations accounts for the lack of knowlege of their bionomics and importance to agriculture and silviculture in the tropics of the new world.

Key to Males of *Docalidia*

1. Style simple, without spines or setae 2

— Style ornate, with spines and/or setae present 6

2(1). Style filamentous in distal half 3

— Style broad in distal half 4

3(2). Pygofer with small caudoventral lobe (Fig. 1); aedeagus with subapical spine (Fig. 3) .... *caterva*, n. sp.

— Pygofer with very long broad caudoventral process (Fig. 19, Nielson 1982b); aedeagus without subapical spine (Fig. 23, Nielson 1982b) .... *exilis* Nielson

4(2). Aedeagus with subapical spine; pygofer with caudodorsal process bifurcate or rounded distally 5

— Aedeagus without subapical spine (Fig. 83, Nielson 1982a); pygofer with caudodorsal process single and pointed (Fig. 79, Nielson 1982a) .... *glabra* Nielson

5(4). Pygofer with caudoventral process very long and lobelike, apex rounded (Fig. 1, Nielson 1982a) .... *lobata* Nielson

— Pygofer with caudoventral process short, narrow, curved mesally and pointed apically (Fig. 31, Nielson 1982a)....... *hansoni* Nielson

6(1). Style with 1–3 spines in distal half to third .. 7

— Style with numerous spines and/or setae in distal half to third 9

7(6). Aedeagus with subapical spine (Fig. 17, Nielson 1982a); style with single, terminal spine (Fig. 14, Nielson 1982a).......... *nuda* Nielson

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— Aedeagus without subapical spine; style with lateral spines 8

8(7). Pygofer with long caudoventral process (Fig. 37, Nielson 1982b); style with long subapical spine directed distally (Fig. 38, Nielson 1982b) .... *hawsi* Nielson

— Pygofer without such process (Fig. 49, Nielson 1982b); style with long spine medially and two short subapical spines directed laterally (Fig. 50, Nielson 1982b) *tuberculata* Nielson

9(6). Pygofer with distinctive long caudoventral process 10

— Pygofer without such process (small lobe often present) 22

10(9). Segment 10 without well-developmed, ornamental ventral processes (often much reduced but apparent) 11

— Segment 10 with well-developed, ornamental ventral processes 12

11(10). Aedeagus with subapical spine (Fig. 64, Nielson 1982a), style with spines in distal half (Fig. 62, Nielson 1982a) .... *paragracilis* Nielson

— Aedeagus without such spine (Fig. 35, Nielson 1982b); style with spines in distal third .... *crista* Nielson

12(9). Style with spines or setae 13

— Style with spines and setae combined 21

13(12). Style with spines only, not densely packed .. 14

— Style with setae only, densely packed appearing as velvet (Fig. 13) .... *vella*, n. sp.

14(13). Style with one to two large medial spines (or near middle) and numerous shorter spines below in distal half 15

— Style without medial spines, numerous spines in distal third 18

15(14). Style with shaft narrow in distal half 16

— Style with shaft expanded in distal third (Fig. 20) .... *zanoli*, n. sp.

16(15). Style with spines below medial spine(s) long and on inner lateral margin 17

— Style with spines below medial spine very short (spiculated) and on dorsal margin (Fig. 74, Nielson 1982a) .... *corneola* Nielson

17(16). Segment 10 with very long ventral processes (Fig. 55, Nielson 1982a); style with single medial spine (Fig. 57, Nielson 1982a) .... *dorsti* Nielson

— Segment 10 with short ventral processes (Fig. 67, Nielson 1982a);style with two medial spines (Fig. 68, Nielson 1982a) .... *bispinata* Nielson

18(14). Pygofer with distally enlarged, caudally truncate, caudodorsal process 19

— Pygofer with bladelike caudodorsal process . 20

19(18). Pygofer with caudodorsal process with teeth in dorsal half (Fig. 7, Nielson 1982c); style with large teeth on inner lateral margin and without vesica in distal third (Fig. 8, Nielson 1982c) .... *multidentata* Nielson

— Pygofer with caudodorsal process with fine serrations on caudal margin (Fig. 23); style with fine teeth or serrations on inner lateral margin and with large bladder or vesica in distal one-eighth (Fig. 27) .... *vesica*, n. sp.

20(18). Pygofer with caudal processes close together (Fig. 30); style with long spines near dorsal margin (Fig. 34) .... *pennyi*, n. sp.

— Pygofer with caudal processes widely separated (Fig. 25, Nielson 1982a); style with short serrations on inner lateral margin (Fig. 26, Nielson 1982a) .... *taylori* Nielson

21(12). Segment 10 with long ventral process extending beyond segment 10 (Fig. 1, Nielson 1982c); plate long and narrow (Fig. 6, Nielson 1982c) .... *breddini* Nielson

— Segment 10 with short ventral process with short, bluntly pointed, subapical secondary process (Fig. 7, Nielson 1982a); plate long and broad (Fig. 12, Nielson 1982a) .... *robertsi* Nielson

22(9). Aedeagus with very short, subapical ventral spine or spine absent 23

— Aedeagus with long, subapical ventral spine . 27

23(22). Aedeagus with ventral spine not more than three times as long as wide 24

— Aedeagus with ventral spine absent 26

24(23). Segment 10 with well-developed ventral processes; style with 1–2 prominent lateral spines on middle of inner lateral margin 25

— Segment 10 with poorly developed ventral processes (Fig. 19, Nielson 1982a); style without such spines (Fig. 20, Nielson 1982a) .... *patula* Nielson

25(24). Segment 10 with long ventral process nearly reaching to apex of segment 10, process terminating with short blunt point (Fig. 1, Nielson 1982b); style with two medial spines before dentate inner margin below (Fig. 2, Nielson 1982b) .... *rema* Nielson

— Segment 10 with shorter ventral process, process reaching to middle of segment 10, process narrowed at distal half and curved dorsally (Fig. 37); style with one medial spine before dentate inner margin below (Fig. 41) .... *triquetra*, n. sp.

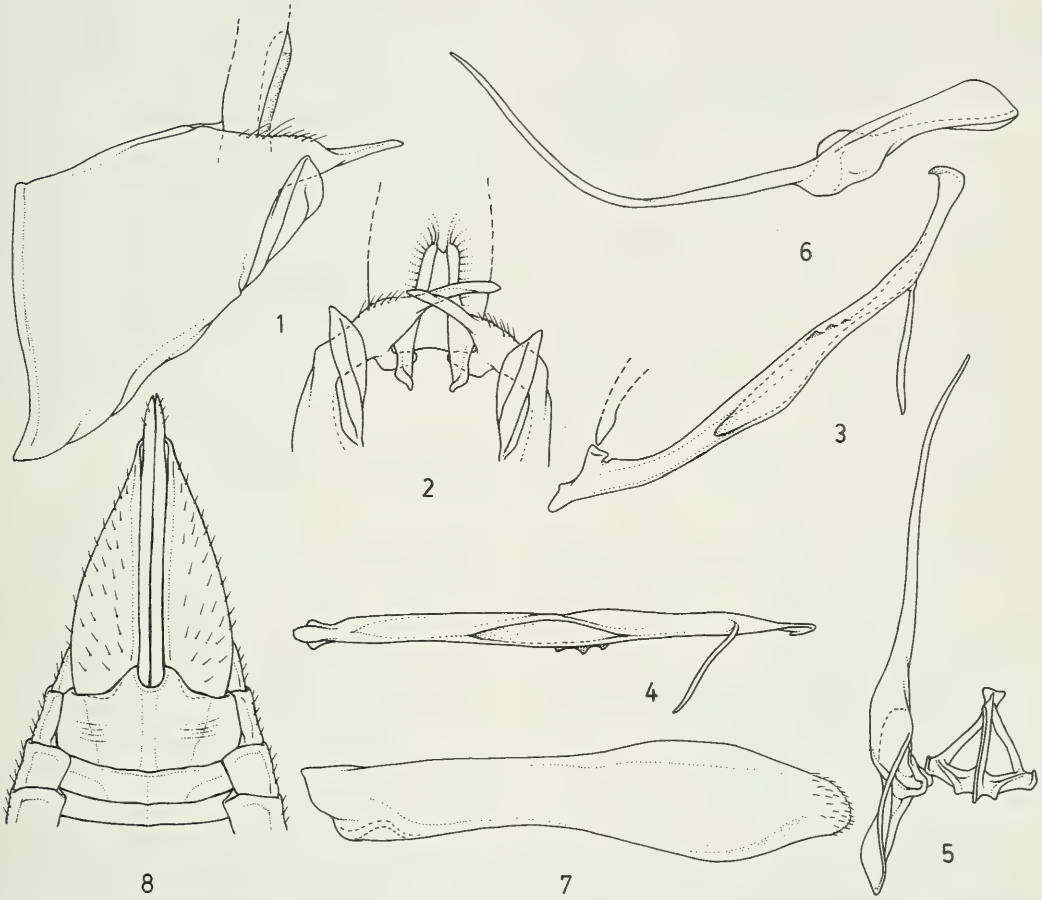
26(23). Style with spines and setae on distal one-fifth, spines on inner lateral margin, setae arranged in one large tuft dorsally (Fig. 26, Nielson 1982b) .... *thola* Nielson

— Style with setae only on distal third, setae on inner and outer lateral margins (Fig. 44, Nielson 1982b) .... *bipenicula* Nielson

27(22). Style with distal half to third with one to two prominent spines and with lateral setae on margins 28

— Style with distal half to third with lateral setae only or with lateral spines only on margins .. 32

28(27). Segment 10 with poorly developed ventral processes; pygofer with straight or nearly straight caudodorsal processes 29



Figs. 1–8. *Docalidia caterva*, n. sp.: 1, Male pygofer and segment 10, lateral view. 2, Segment 10 and pygofer processes, ventral view. 3, Aedeagus, lateral view. 4, Aedeagus, ventral view. 5, Connective and right style, dorsal view. 6, Style, lateral view. 7, Plate, ventral view. 8, Female venter, ventral view.

— Segment 10 with large well-developed ventral process (Fig. 7, Nielson 1982b); pygofer with caudodorsal process decurved apically (Fig. 7, Nielson 1982b) .... *unca* Nielson

29(28). Style with setae occupying distal half, setae long and mostly stout 30

— Style with setae occupying distal third, setae short and fine 31

30(29). Style with prominent medial lobe on inner lateral margin (Fig. 48), aedeagus with broad shaft (Fig. 47) .... *setacea*, n. sp.

— Style without such lobe (Fig. 55), aedeagus with narrow shaft (Fig. 54)..... *gracilitas*, n. sp.

31(29). Style narrow throughout with short, stout spine subapically in dorsal view (Fig. 38, Nielson 1982a) .... *digitata* Nielson

— Style triangulate in distal third with long narrow spine distad of middle in lateral view (Fig. 51, Nielson 1982a) .... *hirsuta* Nielson

32(27). Style with spines only 33

— Style with setae only 34

33(32). Style with convex lobe medially on inner lateral margin, spines confined to medial lobe (Fig. 64).................... *convexa*, n. sp.

— Style not as above, spines occupying entire distal third (Fig. 74)......... *paracrista*, n. sp.

34(32). Style with distal half narrowed throughout .. 35

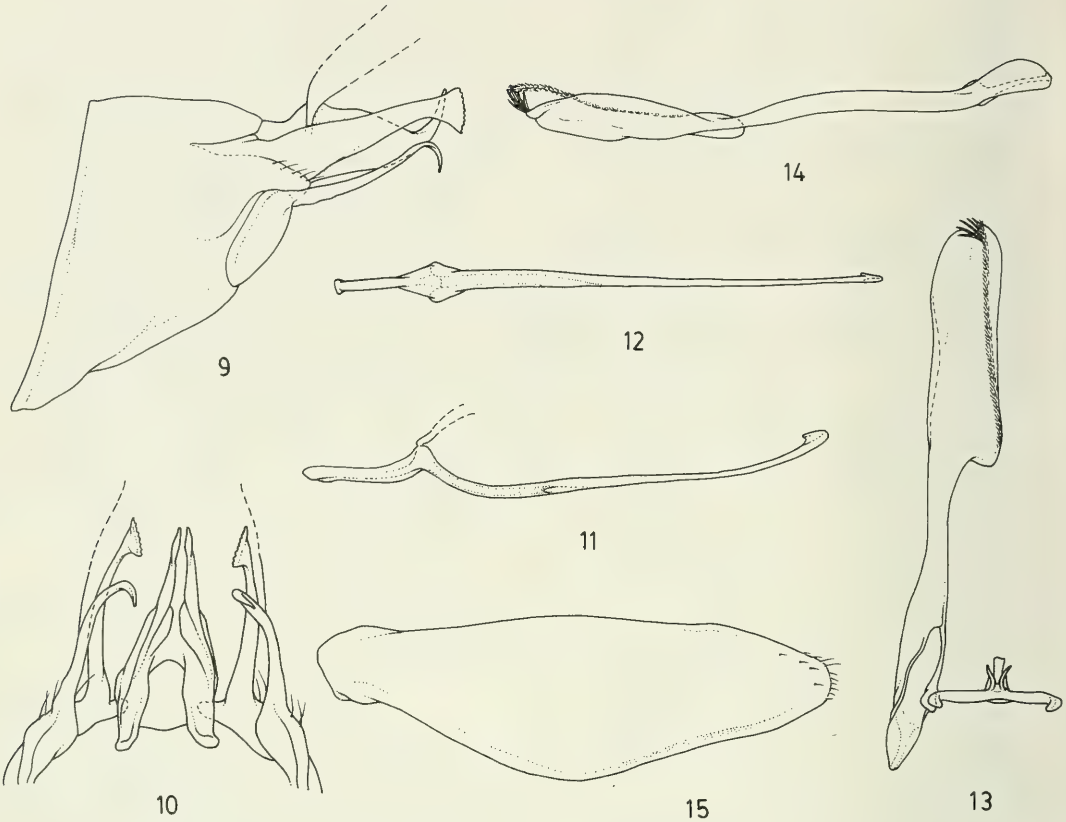
— Style with distal half to third broadly expanded 36

35(34). Style with setae on inner lateral margin from distal three-fourths to apex (Fig. 44, Nielson 1982a) .... *permagna* Nielson

— Style with setae on dorsal margin basal of apex (Fig. 19, Nielson 1982c)...... *subcrista* Nielson

36(34). Style with distal half expanded (Fig. 14, Nielson 1982c); segment 10 without ventral process (Fig. 13, Nielson 1982c)... *lateralis* Nielson

— Style with distal third expanded, triangulate (Fig. 14, Nielson 1982b); segment 10 with short ventral process (Fig. 13, Nielson 1982b) .... *triangulata* Nielson



Figs. 9–15. *Docalidia vella,* n. sp.: 9, Male pygofer and segment 10, lateral view. 10, Segment 10 and pygofer processes, ventral view. 11, Aedeagus, lateral view. 12, Aedeagus, ventral view. 13, Connective and right style, dorsal view. 14, Style, lateral view. 15, Plate, ventral view.

Docalidia caterva, n. sp.

Figs. 1–8

LENGTH.—Male, 5.30 mm, female, 6.40 mm.

Small, robust species. General color black with two narrow, broken, pale, ochraceous transverse bands on forewings (wider in female) and numerous pale to ochre spots on veins and cells, apex pale to ochraceous; crown ochre; eyes reddish brown; pronotum and scutellum black in male, brown in female; face black in male, light brown in female.

Head large, broad, nearly as wide as pronotum; crown short, narrow, much narrower than width of eyes, depressed, lateral margin convergent basally; eyes large, elongate ovoid; pronotum short, slightly longer than crown, inflated; scutellum large, much longer than pronotum, inflated anteriorly; forewings long and broad; clypeus narrow, median clypeal carina well developed; clypellus narrow, lateral margins flared distally.

MALE.—Pygofer in lateral view with very small caudoventral lobe, caudodorsal margin with long narrow process (Figs. 1, 2); segment 10 without ventral processes (Figs. 1, 2); aedeagus asymmetrical, long, nearly tubular, broadly curved in lateral view, with long subapical spine on lateroventral margin and toothed medially on one side of dorsolateral margin (Figs. 3, 4); gonopore very large on lateroventral margin (Fig. 4); style long, very narrow and needlelike in distal half, reaching to about middle of aedeagal shaft (Figs. 5, 6); plate long, narrow, slightly constricted medially, enlarged subapically, and narrowed distally to rounded apex (Fig. 7).

FEMALE.—Seventh sternum large, about two to three times as long as preceding segment, caudal margin produced at middle, with shallow narrow concavity medially and short blunt projection on either side of middle (Fig. 8).

HOLOTYPE (male).—BRAZIL: Am. [Amazonas], Manaus, INPA, 1.V.1976, E. Castellon B. (MZUSP). Allotype female, same data as holotype, except 28.IV.1976 (MZUSP).

REMARKS.—This species is similar in general habitus to *limpidosparsa* (Stal) but is easily separated by the very small caudoventral lobe on the pygofer, by the needlelike style, and by the dentations on the aedeagal shaft.

Docalidia vella, n. sp.

Figs. 9–15

LENGTH.—Male, 6.40 mm.

Small, robust species. General color black except for pale anterior area of crown and narrow, ochre apical margin of forewings.

Head short, broad, much narrower than pronotum; crown broad, about as wide as eye, lateral margins parallel except convergent near base; pronotum short, about as long as crown, inflated; scutellum large, median length greater than median length of pronotum; forewing long and broad; clypeus long and broad; median clypeal carina well developed; clypellus narrow; lateral margins nearly parallel.

MALE.—Pygofer in lateral view with long, narrow, apically decurved caudoventral process (Figs. 9, 10); caudodorsal margin with process as in *vesica* (Fig. 9); segment 10 with ventral processes as in *vesica* (Figs. 9, 10, 23); aedeagus asymmetrical; configuration as in *vesica* except without subapical spine (Figs. 11, 12, 25); style long, nearly as long as aedeagus, basal half narrow, distal half very broad, inner dorsal margin lobed distally, with longitudinal fold along entire inner lateral margin in distal half, this margin densely covered with very short setae giving an appearance of velvet, apex with few weak membranous spines (Figs. 13, 14); plate long and very broad, apex with short macrosetae (Fig. 15).

FEMALE.—Unknown.

HOLOTYPE (male).—PERU: Madre de Dios, Rio Tambopata Res., 30 air km SW Pto. Maldonado, 290 m, subtropical moist forest, 11–15.XI.1979, J. W. Heppner (USNM).

REMARKS.—This species is similar in general habitus and some male genital characters to *vesica* but can be distinguished by the absence of the subapical aedeagal spine and by the velvetlike inner lateral margin in the enlarged distal half of the style.

Docalidia zanoli, n. sp.

Figs. 16–22

LENGTH.—Male, 6.75 mm.

Small robust species. General color dark brown with broad, nearly complete, transverse translucent band on middle of forewings, veins black with pale spots; crown pale; eyes light brown; pronotum and scutellum black with bullae on pronotum pale; face black.

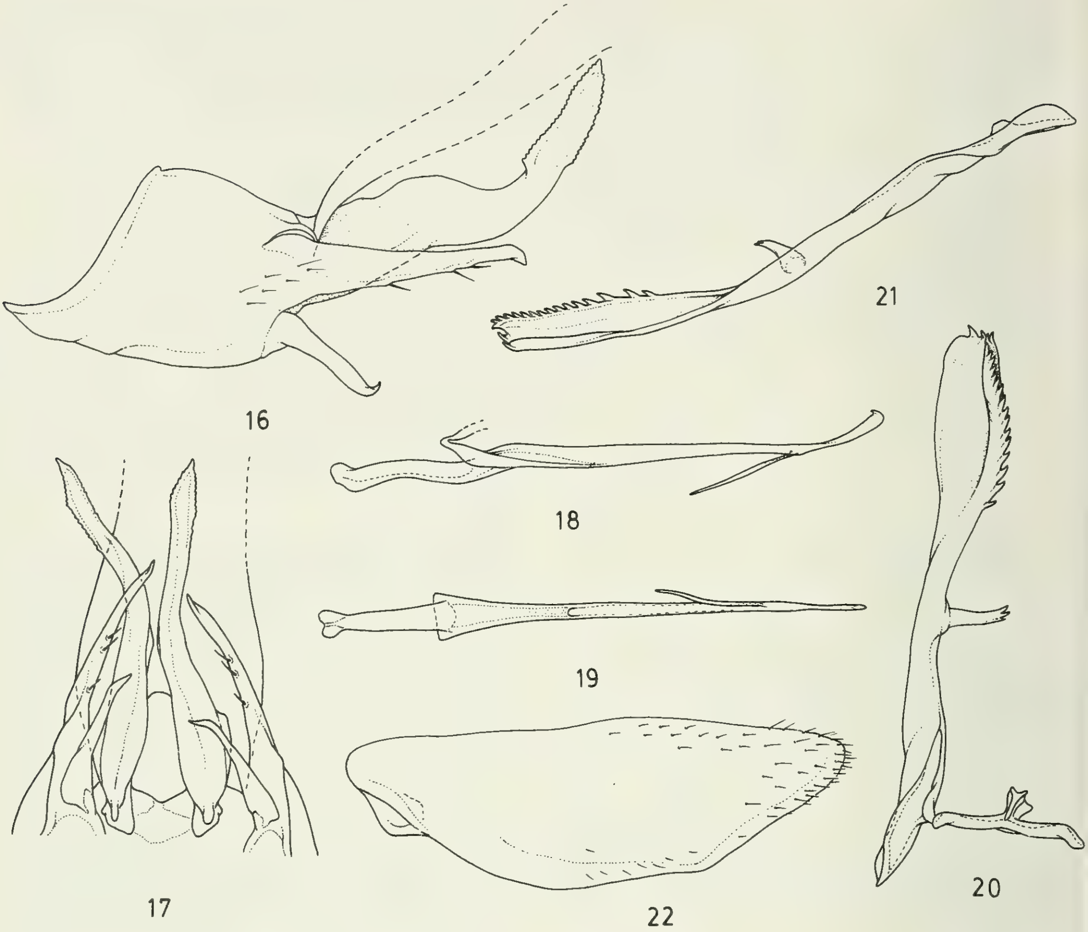
Head short, very broad, slightly narrower than pronotum; crown broad about as wide as eye, depressed, lateral margins as in *gracilitas;* eyes large, semiglobular; pronotum and scutellum as in *gracilitas* except more deeply marked; forewing long and broad; clypeus and clypellus configuration as in *gracilitas*.

MALE.—Pygofer in lateral view with long, narrow, distally curved caudoventral process and with long, narrow caudodorsal process, caudodorsal process longer than caudoventral process (Figs. 16, 17); segment 10 with ventral process very large, broad at basal half, narrowed at distal half, curved caudodorsally and extending to apex of segment 10 (Figs. 16, 17); aedeagus asymmetrical, long, narrow along dorsal margin, broad along ventral margin, slightly curved throughout in lateral view with long, narrow subapical spine on ventral margin (Figs. 18, 19); gonopore basad of middle on ventral margin; style long, reaching to about apex of aedeagus, with medial process on inner lateral margin, process asymmetrically toothed distally, distal third of style expanded, with inner lateral margin serrated and submarginally sclerotized, apex rounded with apical teeth (Figs. 20, 21); plate long and broad, tapered toward bluntly rounded apex (Fig. 22).

FEMALE.—Unknown.

HOLOTYPE (male).—BRAZIL: Cruzeiro do Sul, ACRE, .____.II.1963, M. Alvarenga (UFP).

REMARKS.—This species is similar in male genital characters to *dentatula* (Metcalf), but it can easily be separated by the presence of a



Figs. 16–22. *Docalidia zanoli*, n. sp.: 15, Male pygofer and segment 10, lateral view. 17, Segment 10 and pygofer processes, ventral view. 18, Aedeagus, lateral view. 19, Aedeagus, ventral view. 20, Connective and right style, dorsal view. 21, Style, lateral view. 22, Plate, ventral view.

long medial process on the inner lateral margin of the style. I name this species for Keti Mariá Rocha Zanol, Universidade Federal Do Parana, who has kindly sent me material for study and who is working on the Deltocephalinae of Brazil.

Docalidia vesica, n. sp.

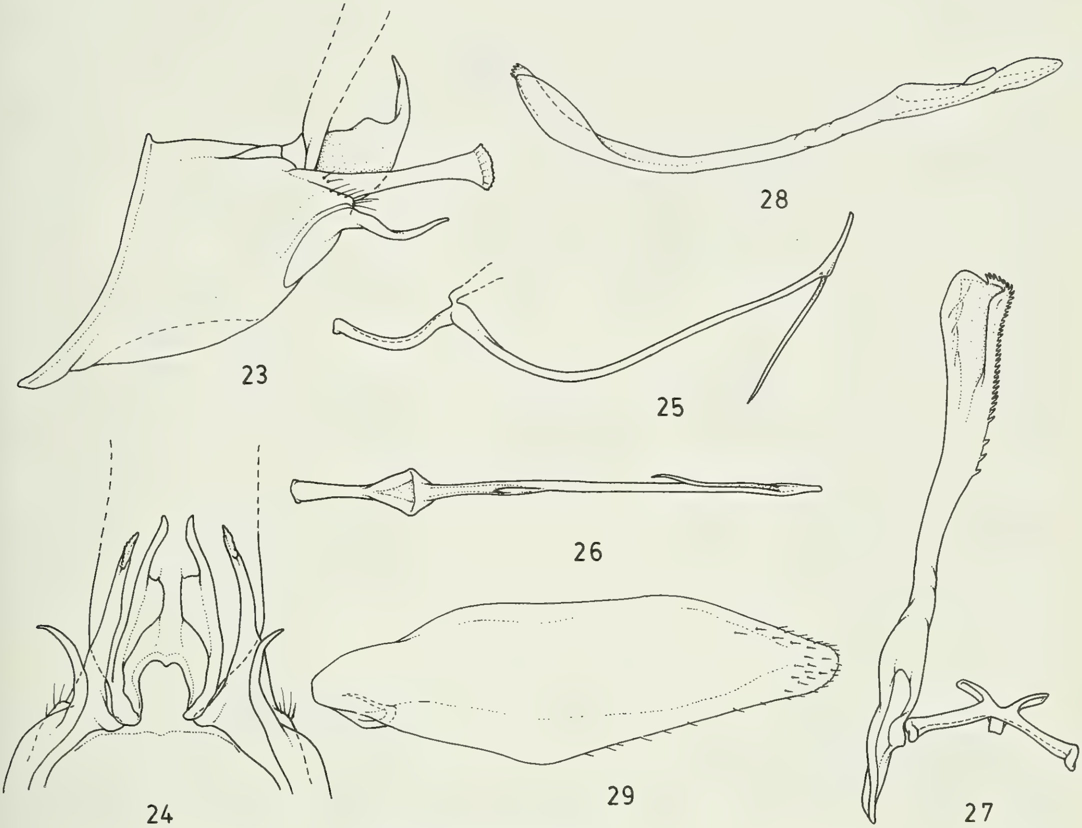
Figs. 23–29

LENGTH.—Male, 6.40 mm.

Medium-sized, robust species. General color black throughout with narrow ochraceous band distally on forewings.

Head short, broad, much narrower than pronotum; crown short, broad, about as wide as eye, depressed on either side of middle, lateral margins parallel except convergent basally; pronotum short, about as long as crown, slightly inflated; scutellum large, median length greater than median length of pronotum; forewing long and broad; clypeus long and broad, median clypeal carina well developed; clypellus narrow, lateral margins slightly expanded distally.

MALE.—Pygofer in lateral view with long, very narrow, sinuate caudoventral process, caudodorsal margin with long, rather stout process, process enalrged distally, caudal margin subtruncate and finely serrate (Figs. 23, 24); segment 10 with well-developed ventral processes, process very broad in basal half, with narrow projection curved dorsally (Figs. 23, 24); aedeagus asymmetrical, long



Figs. 23–29. *Docalidia vesica*, n. sp.: 23, Male pygofer and segment 10, lateral view. 24, Segment 10 and pygofer processes, ventral view. 25, Aedeagus, lateral view. 26, Aedeagus, ventral view. 27, Connective and right style, dorsal view. 28, Style, lateral view. 29, Plate, ventral view.

and nearly needlelike throughout, broadly curved in lateral view, with long subapical spine on ventral margin (Figs. 25, 26); gonopore basad of middle on lateral margin; style very long, extending beyond apex of aedeagus, broad throughout except for constriction along middle, finely toothed in distal third of inner lateral margin and with large, saclike membranous bladder dorsally in distal one-eighth (Figs. 27, 28); plate long and very broad with microsetae distally (Fig. 29).

FEMALE.—Unknown.

HOLOTYPE (male).—PERU: Monson Valley, Tingo Maria, 8.X.1954, E. L. Schlinger and E. S. Ross (CAS).

REMARKS.—*Docalidia vesica* has similar style to *patula* Nielson and similar aedeagus and segment 10 processes to *unca* Nielson but can be distinguished from both species by the long, stout caudodorsal process of the pygofer, which is enlarged distally and truncate and serrate on caudal margin, and by the long sinuate caudoventral pygofer process. It lacks the spines on the middle of the inner margin of style in *unca* and has a much longer subapical aedeagal spine than *patula*.

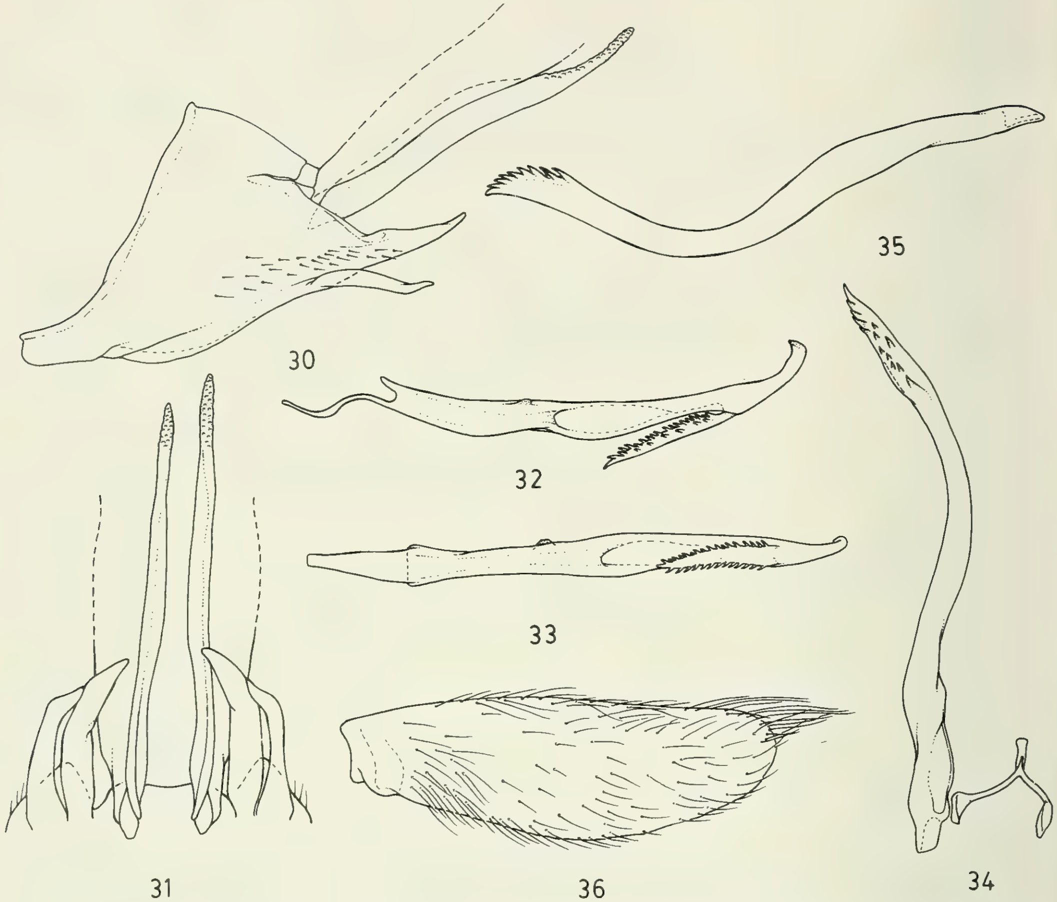
Docalidia pennyi, n. sp.

Figs. 30–36

LENGTH.—Male, 7.75 mm.

Large, robust species. General color brown. Crown deep tan with dark markings; eyes reddish brown; pronotum and scutellum black; forewing brown with broad, deep tan transverse band near middle and along apex.

Head short and very broad, narrower than pronotum; crown short, slightly exceeding anterior margin of eyes, broad, about as wide as eyes; pronotum and scutellum large; forewing broad; clypeus broad with well-



Figs. 30–36. *Docalidia pennyi*, n. sp.: 30, Male pygofer and segment 10, lateral view. 31, Segment 10 and pygofer processes, ventral view. 32, Aedeagus, lateral view. 33, Aedeagus, ventral view. 34, Connective and right style, dorsal view. 35, Style, lateral view. 36, Plate, ventral view.

veloped median longitudinal carina; clypellus narrow, lateral margins expanded distally.

MALE.—Pygofer in lateral view with two long bladelike processes close together on caudodorsal margin, ventral process narrower (Fig. 30); segment 10 with pair of very long, narrow ventral processes that extend beyond apex of segment 10, minutely dentate on dorsal margin and at apex (Figs. 30, 31); aedeagus asymmetrical, long, with longitudinal trough medially on ventral margin, apex curved dorsally in lateral view and with moderately long subapical ventral spine directed basally, spine dentate; gonopore medial on ventral margin (Figs. 32, 33); style very long, nearly reaching apex of aedeagus, narrow, broadly sinuate in lateral view, with numerous spines near dorsal margin on distal one-fourth (Figs. 34, 35); plate long and broad, with numerous, long, microsetae along inner margin and at apex (Fig. 36).

FEMALE.—Unknown.

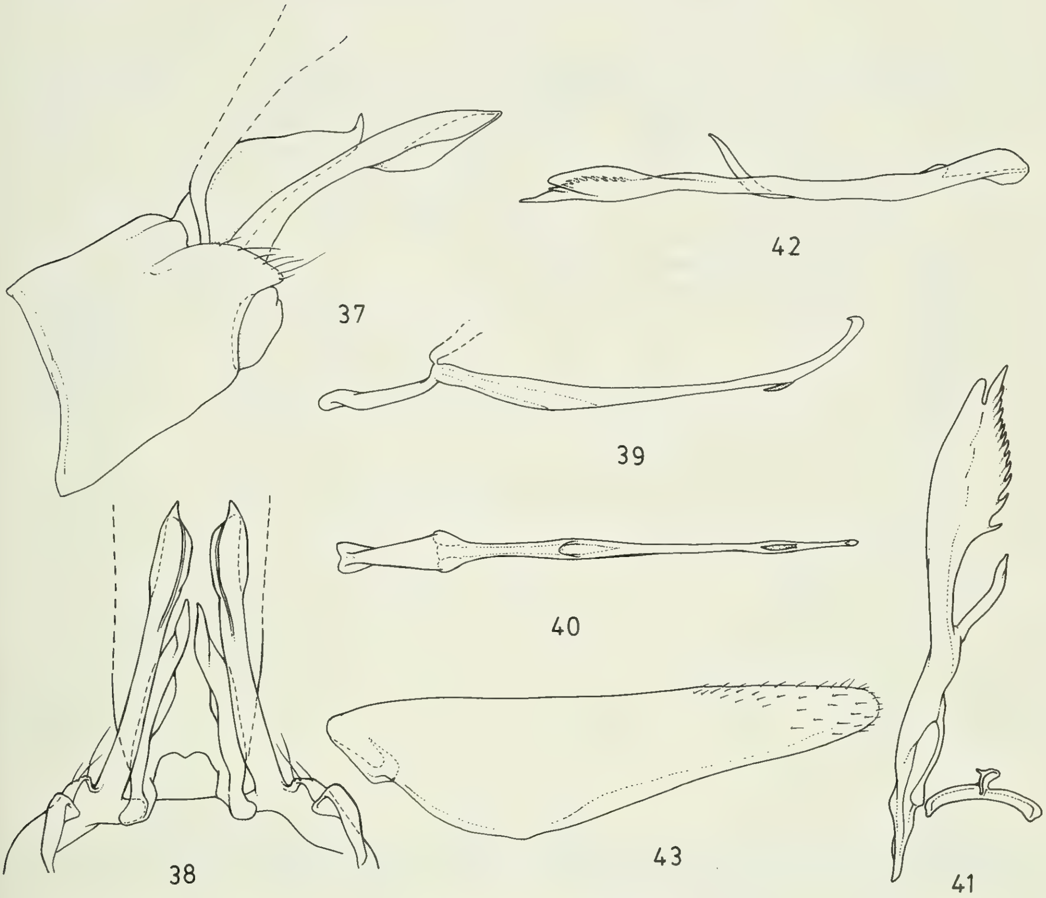
HOLOTYPE (male).—BRAZIL: LeBrea, Amazonas, 27.V.1963. Antonio Carqueira, 2518 (MZUSP).

REMARKS.—This species is near *dentatula* (Metcalf) and can be distinguished by the narrow style with numerous spines on its distal third. I take pleasure in naming this species for Dr. Norman D. Penny, California Academy of Sciences, who has collected several new species of coelidiine leafhoppers described in this and other papers.

Docalidia triquetra, n. sp.

Figs. 37–43

LENGTH.—Male, 6.15 mm.

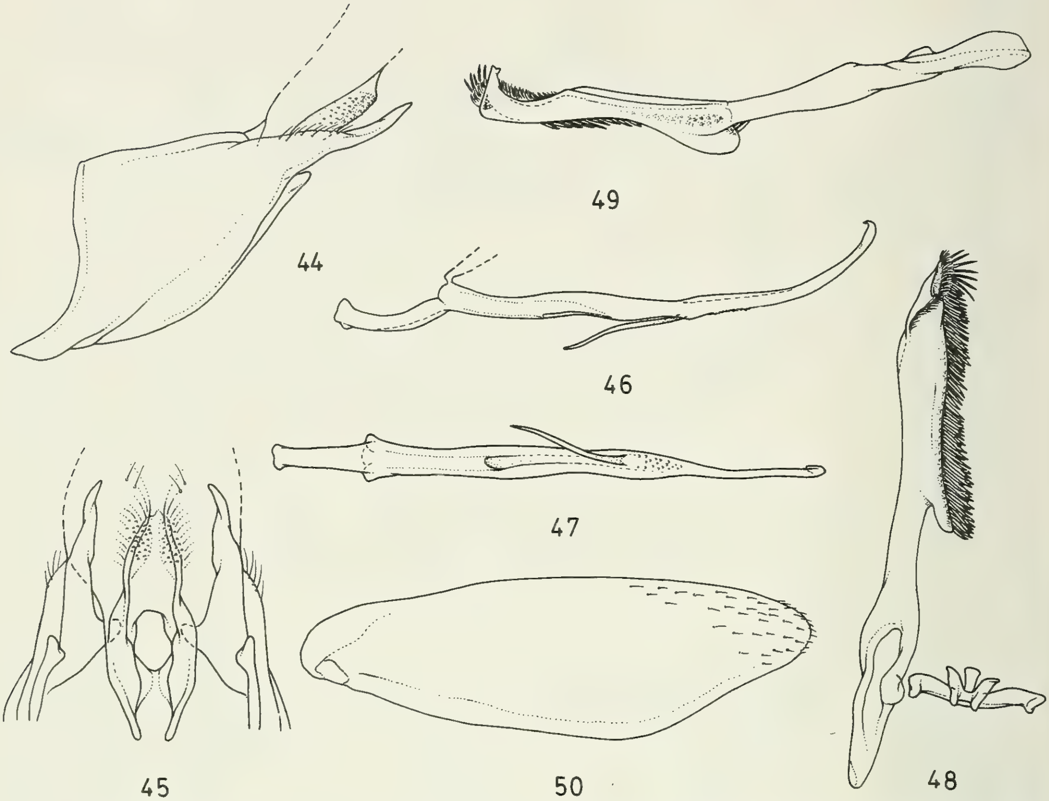


Figs. 37–43. *Docalidia triquetra*, n. sp.: 37, Male pygofer and segment 10, lateral view. 38, Segment 10 and pygofer processes, ventral view. 39, Aedeagus, lateral view. 40, Aedeagus, ventral view. 41, Connective and right style, dorsal view. 42, Style, lateral view. 43, Plate, ventral view.

Small, robust species. General color brown with large, triangular ochre area on middle of forewing; crown pale; eyes reddish brown; pronotum black with ochraceous bullae; scutellum black; veins of forewings with ochre spots; face dark brown.

Head short and very broad, narrower than pronotum; crown short and wide, nearly as wide as eyes, depressed, lateral margins convergent basally; eyes large, semiglobular; pronotum short, about as long medially as crown; scutellum large, median length greater than median length of pronotum; forewing long and broad; clypellus long and broad, with prominent median longitudinal carina; clypellus narrow, lateral margins parallel except for expansion distally.

MALE.—Pygofer in lateral view with very long process on caudodorsal margin, process reaching apex of segment 10, asymmetrically flanged laterally on distal third of ventral margin (Figs. 37, 38); segment 10 with short, basally broad ventral process, process gradually narrowed toward apex, apex curved dorsally to a blunt point (Figs. 37, 38); aedeagus slightly asymmetrical, long, very narrow, compressed laterally at distal two-thirds, broadly curved in lateral view, with very small spine subapically on ventral margin (Figs. 39, 40); gonopore basad of middle on ventral margin; style very long, nearly reaching to apex of aedeagus, ornate at distal half with long lateral process on middle of inner margin, process directed distally and curved dorsally at distal half, distal third of style subtriangular, with lateral teeth on inner margin from base to apex, apex clefted medially, inner part sharply pointed and sclerotized, outer part



Figs. 44–50. *Docalidia setacea*, n. sp.: 44, Male pygofer and segment 10, lateral view. 45, Segment 10 and pygofer processes, ventral view. 46, Aedeagus, lateral view. 47, Aedeagus, ventral view. 48, Connective and right style, dorsal view. 49, Style, lateral view. 50, Plate, ventral view.

narrowly rounded and translucent (Figs. 41, 42); plate long and broad with short, microsetae distally (Fig. 43).

FEMALE.—Unknown.

HOLOTYPE (male).—BRAZIL: Ro [Rondonia], Porto Velho, 11.IX.1965, Epitacio, DPTO Zool., UF Parana (UFP).

REMARKS.—This species is similar to *ferriplena* (Walker) in male genital characters but can be distinguished by the flanged caudodorsal process of the pygofer and by the distal third of the style, which is clefted apically with inner side sharply pointed and outer one rounded.

Docalidia setacea, n. sp.

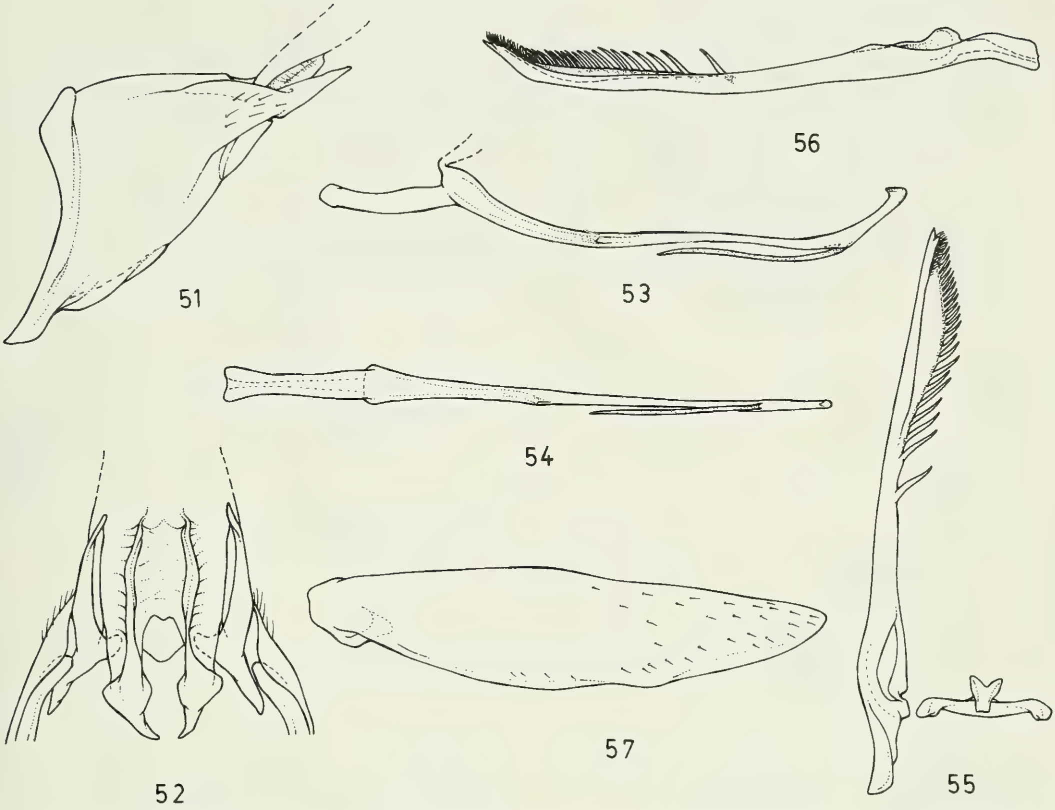
Figs. 44–50

LENGTH.—Male, 8.10–8.30 mm.

Large, robust species. General color deep tan to dark brown throughout; pronotum and scutellum black with numerous small tannish spots; veins of forewings with small suffused spots; face brown to blackish.

Head short, very broad, narrower than pronotum; crown short, broad, about as wide as eye, disk depressed in either side of middle, lateral margins parallel except convergent basally; pronotum short, little longer medially than crown; pronotum large, length greater than length of pronotum; forewing long and broad; clypeus long, narrow, median clypeal carina well developed; clypellus narrow, lateral margins broad distally.

MALE.—Pygofer in lateral view with very small caudoventral lobe, caudodorsal margin with long, narrow process (Fig. 44); segment 10 with poorly developed ventral process (Figs. 44, 45); aedeagus asymmetrical, long, slightly curved dorsally at distal fourth in lateral view, flanged medially on dorsal margin in dorsal view, with long, very narrow ventral spine on middle of shaft (Figs. 46, 47);



Figs. 51–57. *Docalidia gracilitas*, n. sp.: 51, Male pygofer and segment 10, lateral view. 52, Segment 10 and pygofer processes, ventral view. 53, Aedeagus, lateral view. 54, Aedeagus, ventral view. 55, Connective and right style, dorsal view. 56, Style, lateral view. 57, Plate, ventral view.

gonopore basad of middle on ventral margin; style long, not reaching apex of aedeagus, ornate at distal half, inner lateral margin with broad, distally rounded lobe on middle, directed anterio-mesally, with numerous stout setae on inner lateral margin from lobe to subapex of style, apex with narrow, blunt spine directed laterally in lateral view and covered with long microsetae (Figs. 48, 49); plate long and very broad, with few microsetae on distal third (Fig. 50).

FEMALE.—Unknown.

HOLOTYPE (male).—BRAZIL: Rondonia, Porto Velho, 1.VI.1979, J. Campbell (MZUSP). Paratype. One male, same data as holotype except 15.III.1979, D. Need (author's collection).

REMARKS.—*Docalidia setacea* is similar to *multispiculata* Nielson in setal pattern and arrangement on the style but can be distinguished by the presence of a broad process on the middle of the inner margin of the style, by the narrow, blunt spine apically on the style and by the narrower aedeagus.

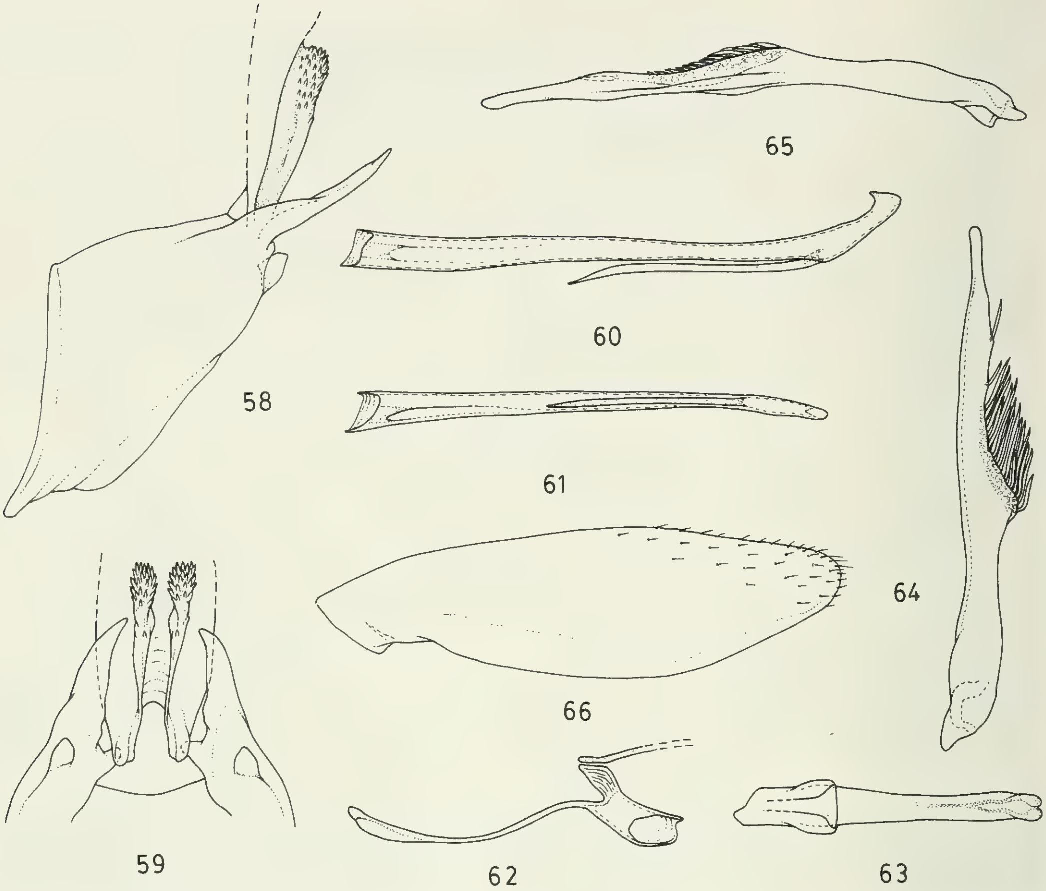
Docalidia gracilitas, n. sp.

Figs. 51–57

LENGTH.—Male, 7.20 mm, female, 7.30–7.50 mm.

Moderate-sized, robust species. General color light brown; pronotum and scutellum dark brown; eyes reddish brown; face brown with black markings.

Head short and very broad, slightly narrower than pronotum, broadly rounded anteriorly; crown short, broad, about as wide as eye, depressed, lateral margins sinuate and converging basally; eyes large, semiglobular; pronotum about as long as crown; scutellum large, median length greater than median length of pronotum; forewing long and broad; clypeus long and broad with prominent me-



Figs. 58–66. *Docalidia convexa*, n. sp.: 58, Male pygofer and segment 10, lateral view. 59, Segment 10 and pygofer processes, ventral view. 60, Aedeagus, distal portion, lateral view. 61, Aedeagus, distal portion, ventral view. 62, Aedeagus, basal portion, lateral view. 63, Aedeagus, basal portion, ventral view. 64, Style, dorsal view. 65, Style, lateral view. 66, Plate, ventral view.

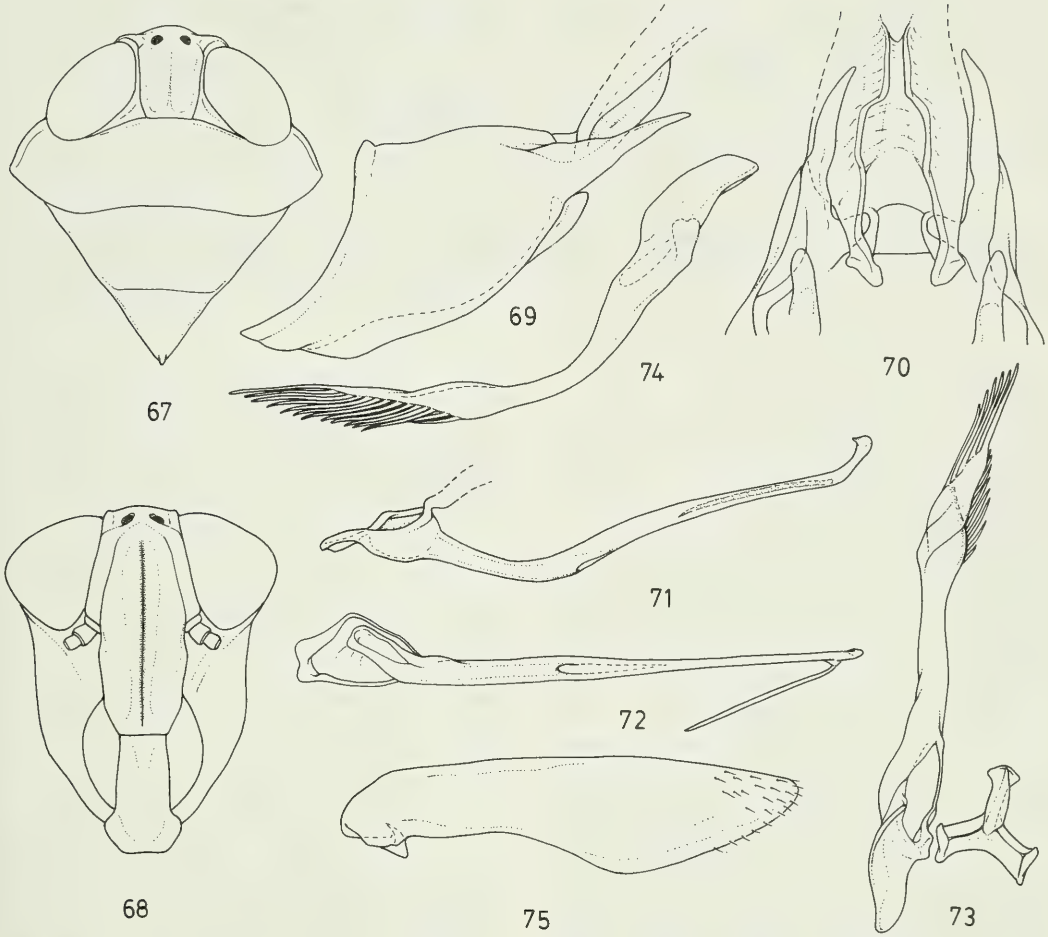
dian longitudinal carina; clypellus narrow, lateral margins sinuate.

MALE.—Pygofer in lateral view with small, narrow caudoventral lobe, caudodorsal margin produced to long, attenuated process (Fig. 51); segment 10 long and narrow with short, inconspicuous ventral lobe (Fig. 51, 52); aedeagus long, very narrow throughout, somewhat compressed laterally, broadly curved in lateral view, with long, very slender, subapical process (Figs. 53, 54); gonopore basad of middle on lateral margin; style long, narrowed medially, expanded at distal half on inner lateral margin on dorsal view, with row of setae from middle of inner margin to apex, setae longer, larger, and wider apart at middle, becoming shorter, narrower, and closer together toward apex, apex with a short, sharp spine (Figs. 55, 56); plate long and broad as in *gracilis* Nielson, with some short microsetae near apex (Fig. 57).

FEMALE.—Seventh sternum large, about three times as long as preceding segment, caudal margin sinuate, lateral margins with submarginal trough.

HOLOTYPE (male).—BRAZIL: Mn. Am. 10.II.1967, Varios 2526 (MZUSP). Allotype female, Amazonas, Manaus, INPA, 30.XII.1977, A. Soares (MZUSP). Paratype, one female, same data as allotype, except 14.V.1979, J. Arias (author's collection).

REMARKS.—From *gracilis*, to which it is similar in male genital characters, *gracilitas* can be distinguished by the narrow caudoventral lobe of the pygofer, by the row of spines on the style that are restricted to the inner



Figs. 67–75. *Docalidia paracrista*, n. sp.: 67, Head, pronotum and scutellum, dorsal view. 68, Face, ventral view. 69, Plate pygofer and segment 10, lateral view. 70, Segment 10 and pygofer processes, ventral view. 71, Aedeagus, lateral view. 72, Aedeagus, ventral view. 73, Connective and right style, dorsal view. 74, Style, lateral view. 75, Plate, ventral view.

lateral margin, and by the pointed style with a short apical spine.

Docalidia convexa, n. sp.

Figs. 58–66

LENGTH.—Male 6.00 mm.

Small, slender species. General color deep brown with broad, pale band medially and narrower pale band apically in forewing; head dark brown; pronotum and scutellum nearly black with small, pale spots on surface; veins of forewings with small, pale spots; face brown.

Head large, narrower than pronotum; crown narrow, width less than width of eye, not depressed, lateral margins convergent basally; pronotum and scutellum apparently short (pin thrust through them); forewing long, narrow, clypeus narrow, median clypeal carina well developed; clypellus narrow, lateral margins expanded distally.

MALE.—Pygofer in lateral view with very small caudoventral lobe, caudodorsal margin with long, narrow, bluntly rounded process (Figs. 58, 59); segment 10 with poorly developed ventral process or flange (Figs. 58, 59); aedeagus asymmetrical (broken subbasally), long, narrow with long subapical spine on ventral margin Figs. 60, 61, 62, 63); gonopore medial on lateral margin; style long, about as long as aedeagus, inner lateral margin convex medially with numerous long spines on middle portion, apical third narrowed to rounded apex (Figs. 64, 65); plate long, narrow, with few microsetae distally (Fig. 66).

FEMALE.—Unknown.

HOLOTYPE (male).—BRAZIL: Mato Grosso, Reserva Humboldt, 10° 11' S 59° 48' O, 22.III.1977. Norman D. Penny (MZUSP).

REMARKS.—This species is near *loricata* (Osborn) but can be differentiated by the poorly developed ventral processes of segment 10, by the convexity on the middle of the inner lateral margin of the style, and by the lack of spines on the apex of the style.

Docalidia paracrista, n. sp.

Figs. 67–75

LENGTH.—Male, 7.25 mm.

Moderate-sized slender species. General color orange with dark markings on costa and subapical areas of forewings, apical margins bordered with brown; crown pale, eyes translucent pale orange; pronotum and scutellum orange; face pale orange.

Head large, distinctly narrower than pronotum (atypical), produced (Fig. 67); crown long, produced, narrower than transocular width, depressed, lateral margins parallel except convergent near base; eyes large, elongate ovoid; pronotum short, median length less than median length of crown; scutellum large, median length greater than length of pronotum; forewing long and narrow with atypical obtusely truncate apex; venation atypical, bases of anteapical cells on same transverse line; clypeus long and narrow, with prominent median longitudinal carina (Fig. 68); clypellus narrow, lateral margins parallel.

MALE.—Pygofer in lateral view with small, elongate caudoventral lobe (Figs. 69, 70); caudodorsal margin with long, narrow process; segment 10 with long, ventrally depressed flange or process (Figs. 69, 70); aedeagus asymmetrical, long, somewhat tubular and sinuate in lateral view, with long subapical spine arising laterally (Figs. 71, 72); gonopore near middle of shaft on ventral margin; style long, slender, nearly reaching apex of aedeagus, broad subdistally with numerous, very long spines on inner lateral margin to narrowed apex, spines of equal length and closely appressed (Figs. 73, 74); plate long and narrow with short microsetae distally (Fig. 75).

FEMALE.—Unknown.

HOLOTYPE (male).—BRAZIL: Rondonia, Vilhena, 02.VIII.1983. Norman Penny (MZUSP).

REMARKS.—*Docalidia paracrista* is similar to *crista* Nielson in male genital characteristics but can be distinguished from it by the general habitus characters and by the small, elongate caudoventral lobe of the pygofer and by the presence of a long subapical spine on the aedeagus.

ACKNOWLEDGMENTS

The material described in this paper, for which I am most grateful, was kindly furnished by the following individuals: Dr. Paul Arnaud, California Academy of Sciences, San Francisco (CAS); Dr. James P. Kramer, U.S. National Museum, Washington, D.C. (USNM); Dr. Norman D. Penny, California Academy of Sciences, San Francisco, who collected specimens while working in Manaus, Brazil, and who sent material from the Instituto Nacional de Pesquisas da Amazonia (the types of specimens from this institute have been sent to the Museu de Zoologia, Universidade de Sao Paulo [MZUSP]); and Keti Mariá Rocha Zanol, Universidade Federal do Parana, Curitiba (UFP).

I appreciate very much the review of the paper by Mr. Ray Gill, California Department of Food and Agriculture, Sacramento, and Dr. Bruce Triplehorn, Liberty University, Lynchburg, Virginia, whose suggestions materially improved its contents. I also thank Jean Stanger for the excellent illustrations.

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FOSSIL BIRDS OF THE OREANA LOCAL FAUNA (BLANCAN), OWYHEE COUNTY, IDAHO

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Abstract.—The Oreana local fauna (Blancan) occurs in exposures of the Glenns Ferry Formation in Owyhee County, Idaho. Fossil birds present include *Phalacrocorax* cf. *P. idahensis*, *Pelecanus* cf. *P. halieus*, an indeterminate anatid, an indeterminate falconid, two species of *Otus*, and a species of *Colaptes* larger than modern *C. auratus* that provides the earliest record of a colaptine woodpecker.

The Oreana local fauna is a Blancan (= Pliocene) assemblage of vertebrate fossils from two localities in southwestern Idaho near the town of Oreana, Owyhee County (IMNH 74001 in Sec 25 and IMNH 74004 (= IMNH 78031) in Sec 1, T4S, R1W; 43 degrees 02′ N Lat., 116 degrees 24′ W Long., Oreana Quadrangle, U.S. Geologic Survey 7.5 minute series topographical map, 1949). Fossils from both localities come from exposures of the Glenns Ferry Formation (Malde et al. 1963) (= Oreana Formation of Anderson 1965) and correlate with the Hagerman local fauna, approximately 75 miles to the east (Conrad 1980). Smith et al. (1982) discuss the biostratigraphy of fishes in this formation.

IMNH 74001 has produced many thousands of complete, disarticulated skeletal elements of fish, along with a few mammal and bird remains from thick lenses of fine sand interbedded with clays. This locality possibly represents a shoreline with swash accumulations (Schaeffer 1972). Vertebrate fossil remains are much more rare from IMNH 74004. More detailed information on each locality is available from IMNH upon request.

Materials and Methods

Comparative material of modern species examined is in collections of the American Museum of Natural History (AMNH), the Idaho Museum of Natural History (IMNH), Pierce Brodkorb (PB), and the National Museum of Natural History, Smithsonian Institution (USNM). All fossil specimens from the Oreana local fauna are in the vertebrate paleontology collections of the IMNH.

Measurements were made with Kanon dial calipers, accurate to 0.05 mm and rounded to the nearest 0.1 mm. BMDP statistical software program BMDP1D was used to calculate simple descriptive statistics (Dixon 1981). Computations were made at the Northeast Regional Data Center (NERDC) at the University of Florida, Gainesville. Anatomical terminology follows Baumel et al. (1979).

Systematic Paleontology

Order Pelecaniformes Sharpe, 1891
Family Phalacrocoracidae (Bonaparte, 1853)
Genus *Phalacrocorax* Brisson, 1760
Phalacrocorax cf *P. idahensis* (Marsh, 1870)

Material.—IMNH 74001/26527, complete left carpometacarpus; IMNH 74004/30221, proximal end of left ulna; 74004/30223, proximal end of right ulna. Tentatively referred.—74004/30224, partial upper mandible; 74004/30222, proximal end of left ulna; 74001/30217, right scapula.

Remarks.—Although originally described from the Hemphillian Chalk Hills Formation (Marsh 1870), this species is better known from the Blancan Hagerman local fauna (Wetmore 1933, Brodkorb 1958, Murray 1970).

The referred upper mandible is short and heavy, having a concave dorsal surface, characteristic of the subgenus *Phalacrocorax* (Howard 1946). The ulnae are within the range of *P. idahensis* or are slightly larger (Murray 1970).

The complete carpometacarpus is larger than any reported by Murray (1970), eliminat-

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TABLE 1. Measurements of humeri of *Otus asio*. Data are mean ± standard deviation (number) and observed range. Measurements are TWSHAFT, transverse width humeral shaft; DSHAFT, depth of humeral shaft; TWDIST transverse width of distal end of humerus; DDIST, depth of distal end of humerus.

	Otus asio		
Measurement	Males	Females	IMNH 28411
TWSHAFT	3.19 ± 0.25 (7) 2.8–3.6	3.37 ± 0.25 (3) 3.1–3.6	3.3
DSHAFT	2.76 ± 0.22 (7) 2.4–3.1	2.87 ± 0.25 (3) 2.6–3.1	2.9
TWDIST	8.66 ± 0.59 (7) 7.9–9.6	9.17 ± 0.67 (3) 8.4–9.6	8.6
DDIST	4.2 ± 0.22 (7) 3.9–4.5	4.90 ± 0.70 (3) 4.4–5.7	4.1

ing the possibility of its being referable to either of the other cormorants reported from the Glenns Ferry Formation, *P. macer* and *P. auritus*, which are smaller. It differs from the carpometacarpus of *P. macropus* by the square shape of the process of metacarpal I (Murray 1970) and by the intermetacarpal tuberosity being in line with the proximal metacarpal symphysis whereas this is more distad in *P. macropus*.

Family Pelecanidae Vigors, 1825
Pelecanus Linnaeus, 1758
Pelecanus cf *P. halieus* Wetmore, 1933

MATERIAL.—74001/26528, nearly complete left femur, lacking medial condyle and caudal portion of lateral condyle. 74004/30225, proximal end of left femur.

DESCRIPTION.—IMNH 26528 is from an immature individual and is abraded. Size intermediate between *P. erythrorhynchos* and *P. occidentalis*. Shaft more robust than in *P. occidentalis*. Neck more distinct, popliteal fossa deeper, undercutting internal condyle, and head angles more proximally than in either *P. occidentalis* or *P. erythrorhynchos*.

REMARKS.—This species was named by Wetmore (1933) from the proximal end of a radius. On the basis of this element it was said to be slightly smaller than *P. o. occidentalis* but probably closely related to *P. erythrorhynchos*. Even with the present material, the systematic position of this poorly known species cannot be clarified.

Order Anseriformes (Wagler, 1831)
Family Anatidae Vigors, 1825
Subfamily Anatinae (Vigors, 1825)
Genus and species indeterminate

MATERIAL.—74001/30504, complete left radius.

REMARKS.—This anatid specimen is similar to the radii in females of *Aythya collaris* but is slightly shorter and more robust. Because the radius is not a diagnostic element in the Anatidae (Woolfenden 1961:2), I have not identified this specimen beyond the level of subfamily.

Order Falconiformes
cf Falconidae Vigors, 1824
Genus and species indeterminate

MATERIAL.—74001/30219, caudal portion of neurocranium.

REMARKS.—Neurocranium preserved from the caudal wall of the orbit caudally, basisphenoid plate missing. Brain case is somewhat bulbous and prominentia cerebellaris is well developed. This skull fragment shows the greatest similarity to the Falconiformes (absence of trabecular bone precludes assignment to the Strigiformes), specifically to the Falconidae. It is similar in size to that of *Falco peregrinus*.

Order Strigiformes (Wagler, 1830)
Family Strigidae Vigor, 1825
Subfamily Striginae (Vigors, 1825)
Genus *Otus* Pennant, 1769
Otus cf *O. asio* (Linnaeus, 1758)

MATERIAL.—IMNH 74001/28411. Distal end of right humerus.

DESCRIPTION.—Similar in size to a male of *O. asio naevius*. Shape of fossa m. brachialis and the shape and development of the epicondylus dorsalis within the range of variation of modern populations of *O. asio*. IMNH 28411 differs from all modern specimens of *O. asio* examined in having a shallower fossa olecrani. See Table 1 for measurements.

REMARKS.—Ford and Murray (1967) reported an indeterminate owl the size of *Otus* *asio* from the Hagerman local fauna. The above specimen may represent the same species.

Otus sp. (Kaup, 1852)

MATERIAL.—IMNH 74001/30216, nearly complete right tarsometatarsus with caudal portion of trochlea IV missing.

DESCRIPTION.—Similar in morphology to female *O. flammeolus* (USNM 554125) but much smaller (skeletons of males of *O. flammeolus* unavailable). Caudal projection of process on trochlea II more developed in fossil. Calcaneal ridge not as inclined laterally.

REMARKS.—The paucity of skeletons of modern species of small owls makes it impossible to determine the exact systematic relationships of this fossil specimen.

Order Piciformes (Meyer and Wolf, 1810)
Suborder Pici Meyer and Wolf, 1810
Family Picidae Vigors, 1825
Subfamily Picinae (Vigors, 1825)
Tribe Colaptini
Genus *Colaptes* Vigors, 1826

GENERIC DIAGNOSIS.—The skull of *Colaptes* may be distinguished from other genera of New World Picinae by the following combination of characters: (1) Interorbital septum completely ossified (similar to *Sphyrapicus, Campethera, Piculus, Celeus,* and *Dinopium*; incompletely ossified or perforate in *Xiphidiopicus, Dendrocopus, Picoides, Veniliornis, Dryocopus, Campe-philus, Picus,* and *Chrysocolaptes*; variable in species of *Melanerpes*); (2) dorsal surface of brain case slightly dimpled (heavily dimpled in *Dryocopus, Campephilus, Picus,* and *Chrysocolaptes*; smooth in *Melanerpes, Sphyrapicus*, and *Xiphidiopicus,* slightly dimpled in other genera examined); (3) supraorbital ridge present (absent to slightly developed in *Melanerpes, Campethera, Dendrocopus, Picus,* and *Dinopium;* present in other genera examined); (4) groove for hyoids present (similar to *Campethera, Piculus, Dryocopus, Campephilus, Picus,* and *Dinopium;* absent to slightly developed in other genera examined); (5) frontals flat to concave (similar to *Melanerpes, Piculus, Celeus, Dryocopus, Campephilus,* and *Chrysocolaptes*; inflated and expanded to varying degrees in other genera examined, producing a distinct, midsagittal crest in *Xiphidiopicus, Campethera, Picus, Din-opium*, and some species of *Picoides*); (6) interorbital constriction narrow (similar to *Celeus* and *Veniliornis*; wide in *Campephilus, Dendrocopus*, and *Sphyrapicus*; intermediate in other genera examined); (7) narrow width between nares (similar to *Melanerpes* and *Dinopium*, wide in *Sphyrapicus, Dendrocopus, Picoides, Veniliornis, Campephilus,* and *Chrysocolaptes*; intermediate in other genera examined); (8) basisphenoid region inflated (not inflated in *Veniliornis, Dryocopus, Campephilus,* or *Chrysocolaptes*, inflated in other genera examined); and (9) otic region inflated (not inflated in *Veniliornis, Campephilus* or *Chrysocolaptes*); inflated to slightly inflated in other genera.

Colaptes sp.

MATERIAL.—IMNH 74001/30218, cranium lacking entire upper jaw, pterygoids, and quadrates.

DESCRIPTION.—IMNH 30218 is distinguished from *Colaptes auratus* and *C. melanochloros* by larger size; from *C. campestris* by having a more developed postorbital process and a deeper, well-defined temporal fossa; from *C. pitius* by having a more bulbous prominentia cerebellaris and a more caudorostrally oriented temporal fossa; and from *C. rupicola* by being smaller and having more distinct hyoid grooves. *Colaptes* (=*Nesoceleus*) *fernandinae* is very distinct from all other species of *Colaptes*. In this species the dorsum of the skull is dimpled, hyoid grooves deep, prominentia cerebellaris poorly developed, and the nuchal crest is well developed. See Table 2 for measurements.

REMARKS.—North American Neogene woodpeckers include *Palaeonerpes shorti* Cracraft and Morony 1969, based on a single distal end of a tibiotarsus from deposits equivalent to the upper part of the Valentine Formation (early Clarendonian). Cracraft and Morony (1969) suggest that the affinities of *Palaeonerpes* are likely to be with the melanerpine woodpeckers rather than with genera such as *Dendrocopos, Dryocopus*, or *Colaptes*.

Pliopicus brodkorbi Feduccia and Wilson 1967, based on a single distal tarsometatarsus, is from the mid- to late Clarendonian Wakeeney local fauna (late Miocene) from the Ogallala Formation, Kansas. Feduccia and Wilson (1967) consider *Pliopicus* to be allied

TABLE 2. Measurements of the crania of species of *Colaptes*. Data are mean, standard deviation, number measured, and observed range. LENGTH, greatest length from the caudal portion of the supraoccipital (*Prominentia cerebellaris*) to the nasofrontal suture, measured on the midsagittal plane (*Planum medianum*); DEPTH, depth of skull from dorsal groove for the hyoid to the slight, anterioposteriorly oriented groove in the basitemporal, measured on the midsagittal plane; WIDTH, greatest transverse width brain case; W-TEMPORAL, transverse width of brain case, measured in the temporal fossa immediately caudal to the postorbital process; W-POSTORB, transverse width between postorbital processes; IORB-CONST, narrowest interorbital constriction; W-IORBSEPT, transverse width interorbital septum; L-FMAG, anteroposterior diameter of *foramen magnum*, measured from the caudad projection of the occipital condyle to the rostral surface with the caudal border of the foramen; W-FMAG, greatest transverse width of *foramen magnum;* W-BULLAE, distance between bullae (i.e., between medial surfaces of *O. exoccipitale ala tympanica*); COND-SR, occipital condyle to sphenoidal rostrum, measured from caudad portion of occipital condyle to the rostralmost extension of the sphenoidal rostrum; EUSTACIAN, distance between openings of the eustacian tubes; W-BASITEMP, greatest transverse width of basitemporal plate; SR-FO, sphenoidal rostrum to ventral border of foramen opticum; FO-PC, foramen opticum to prominentia cerebellaris. ( ) = specimen damaged.

Measurement	*auratus*	*campestris*	*pitius*	*melanochloros*	*rupicola*	*fernandinae*	IMNH 30218
Length	29.33 ± 0.93 (28) 27.5–31.1	31.0	31.7	29.0	32.5; 29.7	31.2	34.1
Depth	17.89 ± 0.42 (28) 17.15–19.15	19.2	19.1	17.2	19.1; 19.2	18.3	19.6
Width	22.39 ± 0.63 (28) 21.3–23.7	22.8	23.9	21.1	24.3; 24.0	—	23.6
W-Temporal	20.75 ± 0.76 (20) 18.9–22.2	20.2	21.4	18.6	21.6; 21.1	(20.6)	21.4
W-Postorb	21.86 ± 0.79 (28) 20.4–22.95	22.9	23.4	21.0	23.4; 22.9	21.8	22.7
Iorb-Const	8.71 ± 0.61 (30) 7.25–9.8	7.7	9.2	9.2	7.8; (7.4)	11.1	(6.7)
W-Iorbsept	1.12 ± 0.13 (19) 0.95–1.55	(1.5)	(1.7)	(1.6)	1.8; 1.7	1.4	1.45
L-FMAG	3.94 ± 0.16 (28) 3.6–4.3	4.1	4.4	3.8	4.2; 3.7	3.7	3.9
W-FMAG	5.76 ± 0.28 (29) 5.35–6.3	5.9	5.4	5.5	6.5; 6.4	6.0	5.65
W-Bullae	10.77 ± 0.44 (29) 10.2–12.0	12.1	11.4	10.5	11.3; 11.0	11.5	11.35
Cond-SR	11.93 ± 0.66 (26) 10.55–13.3	11.4	12.4	10.45	11.9; 12.1	11.6	12.95
Eustacian	3.94 ± 0.30 (27) 3.25–4.75	4.5	4.4	4.8	4.6; 3.2	4.5	4.0
W-Basitemp	13.91 ± 0.51 (27) 13.2–14.95	(13.0)	(11.9)	(11.5)	(11.0); (10.6)	(11.7)	(14.85)
SR-FO	3.84 ± 0.27 (27) 3.25–4.55	4.5	4.2	4.3	3.9; 3.9	4.0	4.55
FO-PC	16.16 ± 0.53 (27) 15.3–17.3	16.5	17.1	15.7	18.0; 17.3	12.4	17.6

to *Melanerpes*. Whereas Cracraft and Morony (1969) reject this suggestion, they could not ally *Pliopicus* with any other particular group of woodpeckers. Brodkorb (1970) described a fossil species of ivory-billed woodpecker, *Campephilus dalquesti*, based on a single distal tarsometatarsus, from the Blancan (Pliocene) Beck Ranch local fauna, Texas, and Feduccia (1975) mentioned the occurrence of *Colaptes* sp. from the Rexroad local faunas, Kansas.

With only a single specimen known, the exact systematic relationships of *Colaptes* sp. from the Oreana local fauna remain uncertain. This specimen may represent either a distinct species or merely a Blancan population of the living *Colaptes auratus* lineage that was larger. Additional specimens of this species are needed to choose between these alternatives. In either case, this record is the earliest known occurrence of a colaptine woodpecker.

DISCUSSION

The Blancan North American Land Mammal Age (= Pliocene) has a diverse fossil avifauna, with approximately 90 avian species reported from 16 localities. Localities in the

Glenns Ferry Formation have produced some 30 of these species (Feduccia 1975 and references therein, Miller 1944, this study). There are also several unstudied collections of fossil birds from this formation (Becker in preparation).

The systematics of many of these species are still poorly known. New species, often only known from fragmentary material, were proposed more on the basis of a presumed difference in geologic time than on quantifiable differences in morphology. Sexual and geographic variation in the osteology of living species was rarely quantified. Many Blancan species of birds should be critically reexamined before being accepted as valid, extinct taxa.

ACKNOWLEDGMENTS

For the loan of material or for access to collections I thank G. Barrowclough and F. Vuilleumier, American Museum of Natural History; J. A. White, Idaho Museum of Natural History; P. Brodkorb, University of Florida; and S. L. Olson, National Museum of Natural History. I thank P. Brodkorb, S. L. Olson, and D. W. Steadman for their comments on this manuscript.

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APPENDIX

Skulls of the following recent woodpeckers were examined to develop the generic diagnosis. *Melanerpes lewis* (1), *M. erythrocephalus* (8), *M. formicivorus* (10), *M. cruenateus* (2), *M. pucherani* (1), *M. chrysogens* (2), *M. (Chryserpes) striatus* (1), *M. (Centurus) hypopolius* (1), *M. radiolatus* (3), *M. rubricapillus* (6), *M. uropygialis* (4), *M. aurifrons* (12), *M. carolinus* (12), *M. caymanensis* (= *supercilliaris*, 3); *Sphyrapicus varius* (9), *S. nuchalis* (2), *S. thyroideus* (2); *Xiphidiopicus percussus* (1); *Campethera bennettii* (1), *C. abingoni* (2), *C. taeniolaema* (1); *Dendropicus fuscescens* (3); *Picoides arizonae* (1), *P. minor* (1), *P. major* (1), *P. scalaris* (4), *P. nuttallii* (1), *P. pubescens* (11), *P. borealis* (9), *P. villosus* (8), *P. trydactylus* (1), *P. arcticus* (2); *Veniliornis fumigatus* (2), *V. sanguineus* (2), *V. cassini* (2); *Piculus flavigula* (2), *P. rubiginosus* (2), *P. auricularis* (1); *Colaptes auratus* (31; *auratus* group—14, *chrysocaulosus* group—3, *cafer* group—12, *chrysoides* group—1; species groups after Short, 1965), *C. campestris* (1), *C. pitius* (1), *C. rupicola* (2), *C. melanochloros* (1), *C. fernandinae* (1), *C. (Chrysoptilus) punctigula* (1); *Celeus undulatus* (2), *C.*

castaneus (1), *C. elegans* (1), *C. flavus* (1); *Dryocopus lineatus* (3), *D. pileatus* (10), *D. martius* (1); *Campephilus guate-malensis* (1), *C. rubricollis* (1), *Picus canus* (1), *P. viridis* (2); *Dinopium javenense* (2), *D. benghalense* (2); *Chrysocolaptes lucidus* (1).

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